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Editor—DR. JOHN CALLAWAY
Dept. of Environmental Science
University of San Francisco
2130 Fulton Street
San Francisco, CA 94117-1080
callaway@usfca.edu

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CONTRIBUTIONS TOWARD A BRYOFLOREA OF CALIFORNIA: I. A SPECIMEN-BASED CATALOGUE OF MOSSES

DANIEL H. NORRIS

University Herbarium, University of California, Berkeley, CA 94720-2465

JAMES R. SHEVOCK¹

Department of Botany, California Academy of Sciences,
San Francisco, CA 94118-4599

ABSTRACT

This catalogue documents 596 mosses for California with 111 taxa newly reported for the state. Thirty taxa previously reported for California have been excluded. The California moss flora is comprised of 163 genera in 49 families. A new combination, *Lescuraea pallida*, is proposed.

Key Words: California mosses, floristics, moss distribution, bryogeography.

It has been over 50 years since a catalogue of mosses was last published for California (Koch 1950a). This present catalogue is based on specimens with every entry supported by one or more herbarium collections that we have examined and cite in the present paper. It is not our intent to produce a range, habitat, or distribution analysis for each taxon based on herbarium records, nor to list all collections available for each entry, but rather to validate and document each species presence and geographic distribution in California. Mosses occur in all 58 counties of the state yet the number of taxa recorded per county varies markedly based on county size, elevational relief, diversity of habitats, climate, and the efforts by bryologists to document its bryoflora (Shevock 2003). Several mosses are known to occur in California from solitary occurrences or from only a handful of specimens. When possible we provide up to six representative collections per taxon. Where applicable, we have preferentially selected specimens obtained from public lands (Bureau of Land Management, National Forests, State Parks, U.S. Fish and Wildlife Service Refuges, State Forests, State Parks, State Fish and Game Ecological Preserves, County Parks, etc.). We do this because these are occurrences likely to remain extant through habitat protection or by conservation efforts within agency management mandates. For those mosses that are considered rare, threatened or sensitive by either the California Native Plant Society or by state and federal agencies, we have listed all occurrences known to us based on our review of specimens.

It has been a long-standing challenge to develop concise statements to accommodate where particular plants can be expected to occur in California. The state is highly complex both geologically and

physiographically. In addition California contains an unusual diversity of habitats, plant communities, and microenvironments for the establishment of moss populations. No previously published distribution system has been developed for California mosses. After reviewing several strategies to address species distribution patterns, we chose to follow the geographic system used by *The Jepson Manual* (Hickman 1993). This hierarchical system of geographic units is four-tiered and comprised of provinces, regions, subregions and districts. The provinces are broadly defined and each province is divided into regions. California has three provinces and ten regions within its boundary. Subregions and districts further define these units. However, based on the state of our understanding and knowledge of mosses in California, we have limited species distributions to the regional level of analysis within this paper. Of the ten geographic subdivisions of California (Hickman 1993), six represent the California Floristic Province, two lie within the Great Basin Floristic Province and two in the Desert Province (Fig. 1). Where a taxon is not restricted to a single geographic subdivision of California (Hickman 1993), we have selected specimens that display a broader geographic range reflecting the unusual diversity of climates and habitats in the state. Our priority selections for broad geographic subdivisions are 1) Sierra Nevada, 2) Klamath/Cascade Ranges, 3) Coast Ranges, 4) Transverse/Peninsular Ranges, and 5) Desert/Great Basin. Collectively, these regions outline the broad physiographic and biologic geography of California. Each moss in this catalogue is listed by region, and we document its presence by a voucher specimen. Clearly some regions are less frequently cited than others. In many cases, this is merely a reflection of collecting habits of bryologists where the senior author has concentrated collecting activities in the north-west portion of the state while the junior author has focused on mosses within the Sierra Nevada. None-

¹ Author for correspondence, e-mail: jshevock@calacademy.org.

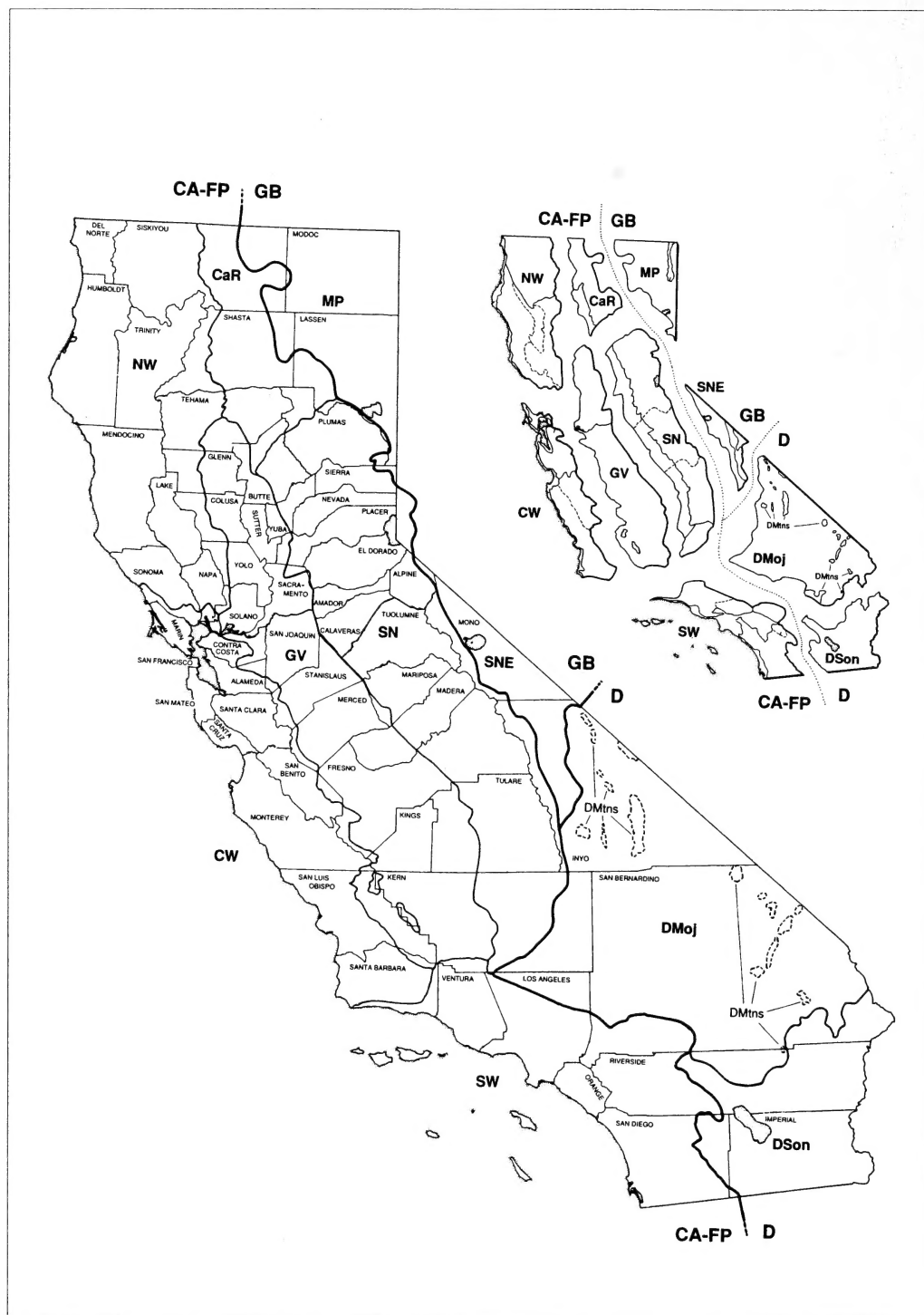


FIG. 1. Geographic subdivisions of California. **California Floristic Province (CA-FP)**: Regions: **CaR** = Cascade Range; **CW** = Central Western California; **GV** = Great Valley; **NW** = Northwestern California; **SN** = Sierra Nevada; **SW** = Southwestern California. **Great Basin Floristic Province (GB)**: Regions: **MP** = Modoc Plateau; **SNE** = East of Sierra Nevada. **Desert Province (D)**: Regions: **DMoj** = Mojave Desert; **DSon** = Sonoran Desert.

theless, a quick visualization of the distribution pattern will provide the reader with a good indication if a species is widespread in California or confined to only a few regions of the state.

The California moss catalogue (Appendix I) provides an updated list of taxa with two key elements: 1) references to mosses reported for California in the published literature, and 2) mosses documented by herbarium specimens as occurring in California that we believe are published here for the first time. In the literature field we reference the pertinent published sources (checklists, bryofloras, and monographs) for each taxon that has been attributed to California prior to this effort. We also have referenced the name used in each publication if it differs from the name preferred in our catalogue. Moss collections at CAS and UC were the primary source for this study, however, we also examined specimens at MO, NY, SBBG, SD and California State University herbaria, especially SFSU. The collections at LAM would have been especially interesting to study primarily for their coverage of southern California. Unfortunately the LAM collections were in storage and not readily available during the course of our herbarium review, however, many duplicates of Fay MacFadden collections were located at MO and UC. The senior author has made more than 35,000 collections in pursuit of developing a moss flora for the state of California. Norris collections cited in this paper reside at UC; and Shevock collections are at CAS. For specimens cited by other collectors, we list the herbaria where their specimens reside. Additions to the moss flora of California that have not been published previously are highlighted with an asterisk. Taxa erroneously reported for the state are placed in Appendix II. Appendix III includes taxa currently not known in California whose presence is documented and verified by voucher specimens generally within 50 miles of the state border. These taxa are listed in the catalogue with the hope that additional field work by bryologists and plant enthusiasts may document occurrences in California in the near future. Appendix IV provides a list of synonyms and excluded names.

Another feature of this catalogue is a literature reference for representative moss illustrations. Used in conjunction with keys to identify California mosses, illustrations are useful in confirming the identification of specimens. We have attempted to reference illustrations from journals and bryofloras that are likely to be in major university libraries and scientific institutions; however, some excellent illustrations are also located in infrequently encountered publications. We hope this feature of the catalogue will be of value for those seeking a good illustration for a particular species.

Nomenclature in bryology continues to undergo considerable modification and realignment as more taxa receive detailed study and monographic treatments. In this catalogue, we generally follow the

nomenclature presented in the checklist for North America prepared by Anderson et al. (1990) and Anderson (1990) along with Crosby et al. (2000). We have generally followed Zander (1993) for generic recognition in the Pottiaceae. We basically follow the family arrangement as presented by Buck and Goffinet (2000). In addition, other name changes and taxonomic inventions are also considered from recently published sources including treatments for the forthcoming bryophyte volumes for the Flora of North America Project (BNFA) along with our own views regarding the circumscription of bryological taxa. Bryological work continues to reassort familial and generic alignments. We respond to these newer treatments by slowly evaluating our acceptances and rejections. Such recent excellent works as Ignatov and Huttunen (2002) have made so many realignments that we find a need to delay advocacy until after this present paper. We have also chosen not to recognize varietal and subspecific ranks in this catalogue but instead list at the species level nearly all taxa that we deem worthy of recognition. In all cases, however, names used in older literature documenting the distribution of mosses in California are referenced to the nomenclature selected for this catalogue (see Appendix IV).

Students of California bryology require not only the distributional literature and illustrations but they also will require additional pertinent literature involving ecology and geography. Monographic and taxonomic literature will also be necessary to these students, and sometimes certain morphologic literature will allow understanding of features seen in mosses.

Ecology literature. Albert 1988; During 1979; Forman 1962; Gignac 2001; Glime and Vitt 1987; Hartman 1969; Janssens and Zander 1980; Jones 1970; Nash et al. 1977; Nichols 1910; Persson 1956; Schatz 1955; Shaw 1981b; Shaw and Owens 1995; Smith 1982; Wilkins 1977.

Geography literature. Austin 1877a, b, 1878; Barnes 1891; Bowers et al. 1974; Christy 1980; Christy and Harpel 1997; Christy et al. 1982; Crum 1972; Delgadillo 1996; Koch 1952, 1954a, 1956; McIntosh 1989, 1997; Norris 1997; Schofield 1969a, 1980, 1984, 1994a; Schofield and Crum 1972; Shaw and Snider 1995; Spence 1988b; Stark and Whittemore 2000; Steere 1969; Zander and Hoe 1979.

Taxonomic literature. Cao and Churchill 1995; Clarke and Duckett 1979; Crosby 1980; Giles 1990b; Greene and Harrington 1988, 1989; Iwatsuki 1981; Jamieson 1980; Koch 1949b; Robinson and Ignatov 1997; Sayre 1946; Shaw 1981c, d, f, 1985; Spence 1996; Taylor and Levitan 1980; Weber 1976; Zander 1978a.

Monographic literature. Anderson and Bryan 1958; Andrews 1913; Andrus 1983; Barkman 1963;

TABLE 1. SYNOPSIS OF THE MOSS GENERA AND FAMILIES OCCURRING IN CALIFORNIA.

| | |
|---------------------------|------------------------|
| Amblystegiaceae | <i>Atractylocarpus</i> |
| <i>Amblystegium</i> | <i>Campylopodiella</i> |
| <i>Hygroamblystegium</i> | <i>Campylopus</i> |
| <i>Leptodictyum</i> | <i>Cynodontium</i> |
| Andreaeaceae | <i>Dichodontium</i> |
| <i>Andreaea</i> | <i>Dicranella</i> |
| Archidiaceae | <i>Dicranum</i> |
| <i>Archidium</i> | <i>Kiaeria</i> |
| Aulacomniaceae | <i>Oncophorus</i> |
| <i>Aulacomnium</i> | <i>Orthodicranum</i> |
| Bartramiaceae | Ditrichaceae |
| <i>Anacolia</i> | <i>Ceratodon</i> |
| <i>Bartramia</i> | <i>Distichium</i> |
| <i>Conostomum</i> | <i>Ditrichum</i> |
| <i>Philonotis</i> | <i>Pleuridium</i> |
| Brachytheciaceae | <i>Trichodon</i> |
| <i>Bestia</i> | Encalyptaceae |
| <i>Brachythecium</i> | <i>Encalypta</i> |
| <i>Eurhynchium</i> | Ephemeraceae |
| <i>Homalothecium</i> | <i>Ephemerum</i> |
| <i>Isothecium</i> | Fabroniaceae |
| <i>Kindbergia</i> | <i>Fabronia</i> |
| <i>Platyhypnidium</i> | Fissidentaceae |
| <i>Pseudoscleropodium</i> | <i>Fissidens</i> |
| <i>Scleropodium</i> | Fontinalaceae |
| <i>Steerecleus</i> | <i>Dichelyma</i> |
| <i>Trachybryum</i> | <i>Fontinalis</i> |
| Bruchiaceae | Funariaceae |
| <i>Bruchia</i> | <i>Entosthodon</i> |
| <i>Trematodon</i> | <i>Funaria</i> |
| Bryaceae | <i>Physcomitrella</i> |
| <i>Anomobryum</i> | <i>Physomitrium</i> |
| <i>Bryum</i> | <i>Pyramidula</i> |
| Buxbaumiaceae | Gigaspermaceae |
| <i>Buxbaumia</i> | <i>Lorentziella</i> |
| Campyliaceae | Grimmiaceae |
| <i>Campylium</i> | <i>Coscinodon</i> |
| <i>Conardia</i> | <i>Grimmia</i> |
| <i>Drepanocladus</i> | <i>Jaffuelobryum</i> |
| <i>Hamatocaulis</i> | <i>Racomitrium</i> |
| <i>Hygrohypnum</i> | <i>Schistidium</i> |
| <i>Pseudo-calliargon</i> | Hedwigiaceae |
| <i>Sanionia</i> | <i>Hedwigia</i> |
| <i>Straminergon</i> | <i>Pseudobraunia</i> |
| <i>Warnstorfia</i> | Helodiaceae |
| Cratoneuraceae | <i>Helodium</i> |
| <i>Cratoneuron</i> | <i>Palustriella</i> |
| Cryphaeaceae | Hookeriaceae |
| <i>Dendroalsia</i> | <i>Hookeria</i> |
| Discoliaceae | Hylocomiaceae |
| <i>Discelium</i> | <i>Hylocomium</i> |
| Dicranaceae | <i>Rhytidiadelphus</i> |
| <i>Arctoa</i> | <i>Rhytidiopsis</i> |
| | Hypnaceae |
| | <i>Buckiella</i> |
| | <i>Calliargonella</i> |

TABLE 1. CONTINUED.

| | |
|----------------------------|---------------------------|
| <i>Dacryophyllum</i> | <i>Pogonatum</i> |
| <i>Herzogiella</i> | <i>Polytrichastrum</i> |
| <i>Homomallium</i> | <i>Polytrichum</i> |
| <i>Hypnum</i> | Pottiaceae |
| <i>Isopterygiopsis</i> | <i>Acaulon</i> |
| <i>Isopterygium</i> | <i>Aloina</i> |
| <i>Platydictya</i> | <i>Barbula</i> |
| <i>Pseudotaxiphyllum</i> | <i>Bryoerythrophyllum</i> |
| <i>Tripterocladium</i> | <i>Crossidium</i> |
| <i>Vesicularia</i> | <i>Crumia</i> |
| Leptodontaceae | <i>Didymodon</i> |
| <i>Alsia</i> | <i>Eucladium</i> |
| Leskeaceae | <i>Gymnostomum</i> |
| <i>Claopodium</i> | <i>Hennediella</i> |
| <i>Leptopterigynandrum</i> | <i>Hymenostylium</i> |
| <i>Lescuraea</i> | <i>Leptophascum</i> |
| <i>Leskea</i> | <i>Microbryum</i> |
| <i>Pseudoleskeella</i> | <i>Molendoa</i> |
| Leucodontaceae | <i>Oxystegius</i> |
| <i>Antitrichia</i> | <i>Phascum</i> |
| <i>Pterogonium</i> | <i>Pseudocrossidium</i> |
| Meesiaceae | <i>Scopelophila</i> |
| <i>Leptobryum</i> | <i>Stegonia</i> |
| <i>Meesia</i> | <i>Syntrichia</i> |
| Mielichhoferiaceae | <i>Timmia</i> |
| <i>Mielichhoferia</i> | <i>Tortella</i> |
| <i>Schizymenium</i> | <i>Tortula</i> |
| Mniaceae | <i>Trichostomum</i> |
| <i>Epipterygium</i> | <i>Triquetrella</i> |
| <i>Leucolepis</i> | <i>Weissia</i> |
| <i>Mnium</i> | Pterigynandraceae |
| <i>Plagiomnium</i> | <i>Heterocladium</i> |
| <i>Pohlia</i> | <i>Myurella</i> |
| <i>Rhizomnium</i> | <i>Pterigynandrum</i> |
| <i>Roellia</i> | Ptychomitriaceae |
| Neckeraceae | <i>Ptychomitrium</i> |
| <i>Bryolawtonia</i> | Rhabdoweisiaceae |
| <i>Metaneckera</i> | <i>Amphidium</i> |
| <i>Neckera</i> | Scouleriaceae |
| <i>Porotrichum</i> | <i>Scouleria</i> |
| <i>Thamnobryum</i> | Seligeriaceae |
| Orthodontiaceae | <i>Blindia</i> |
| <i>Orthodontium</i> | <i>Dicranoweisia</i> |
| Orthotrichaceae | Sematophyllaceae |
| <i>Orthotrichum</i> | <i>Sematophyllum</i> |
| <i>Ulota</i> | Sphagnaceae |
| <i>Zygodon</i> | <i>Sphagnum</i> |
| Plagiotheciaceae | Tetraphidaceae |
| <i>Plagiothecium</i> | <i>Tetraphis</i> |
| Polytrichaceae | Timmia |
| <i>Atrichum</i> | <i>Timmia</i> |
| <i>Meiotrichum</i> | |

TABLE 2. THE TEN LARGEST MOSS FAMILIES IN CALIFORNIA.

| | |
|------------------|----|
| Pottiaceae | 93 |
| Grimmiaceae | 61 |
| Brachytheciaceae | 50 |
| Bryaceae | 42 |
| Mniaceae | 37 |
| Orthotrichaceae | 35 |
| Dicranaceae | 32 |
| Campyliaceae | 25 |
| Sphagnaceae | 23 |
| Hypnaceae | 18 |

Bartlett and Vitt 1986; Bartram 1924; Best 1897, 1900; Brassard 1969, 1984; Bremer 1980a, b, 1981; Brotherus 1908; Bryan 1997; Corley 1978; Crum 1965a, b, 1997; Crundwell 1957; Crundwell and Nyholm 1964; Delgadillo 1973; Eckel 1997b; Eckel et al. 1997; Flowers 1952; Frahm and Isoviita 1988; Frahm and Vitt 1978; Frye 1917a, b, 1918a, b; Giles 1990a; Gradstein and Sipman 1978; Grevén 1994, 1995, 1999a, b, 2003; Hedenäs 1993b, 1996a, b, 1997a, b, c; Ireland 1969a, b, 1985, 1986; Iwatsuki 1981; Koch 1954b; Koponen 1968a, b; Lawrey 1948; Lewinsky 1993; Lewinsky and Hedenäs 1998; Lawton 1972; Ochyra 1982, 1998b; Piippo 1983; Pursell 1994; Robinson 1970, 1976; Saito 1972, 1973; Sayre 1952; Spence 1987; Stark 1996; Steere 1939, 1940a, b, c, d; Stoneburner 1985; Vitt 1972; Williams 1919; Zales 1973; Zander 1981b, 1989, 1998.

Morphologic literature. Allen 1983; Crum 1971, 2001; Field 1963; Goffinet et al. 1999; Griffin 1998; Hill 1902; Ireland 1971; Mueller 1973; Shaw and Crum 1984; Zander 1979b, 1980.

A synopsis of the moss genera and families for California is provided in Table 1. The 10 largest moss families in California include over two-thirds of the species documented for the state (Table 2). On the other end of the spectrum, 11 moss families are represented by a single species in California. The 10 largest moss genera in California are in seven families, and they represent nearly 38 percent of the species recorded for the state (Table 3).

PREVIOUS WORKS

While published references for mosses occurring along the Pacific Coast of North America date back to the late 1800's (Sullivant 1856, 1864; Hampe 1860; Lesquereux 1865, 1868), the first floristic treatment of California mosses with identification keys appeared in volume II of *Botany of California* (Watson 1880). This work, based primarily on the collections of Bigelow, Bolander, and Brewer, listed 181 mosses for California with comments and references on 79 additional mosses thought to be probable based on specimens obtained in adjacent states or in habitats also known to occur in California. Watson built on the work of Sullivant (1856) and

TABLE 3. THE TEN LARGEST MOSS GENERA IN CALIFORNIA.

| | |
|----------------------|----|
| <i>Bryum</i> | 41 |
| <i>Orthotrichum</i> | 30 |
| <i>Grimmia</i> | 29 |
| <i>Sphagnum</i> | 23 |
| <i>Brachythecium</i> | 22 |
| <i>Pohlia</i> | 19 |
| <i>Racomitrium</i> | 18 |
| <i>Didymodon</i> | 14 |
| <i>Syntrichia</i> | 14 |
| <i>Tortula</i> | 14 |

Lesquereux (1868) that cumulatively accounted for 177 mosses for California. As collecting continued in the early part of the 20th century, many new moss records for California were subsequently published in the *Moss Flora of North America* (Grout 1928–1940). Koch (1950a) systematically reviewed the herbarium record for mosses attributed to California. He added 39 mosses as new state records based primarily on his collections. His studies concluded that California had 317 mosses verified by specimens, 20 species of doubtful occurrence, and he excluded 68 mosses previously reported for California (Koch 1950a, 1954a). Koch also provided the first detailed assessment of the distribution of mosses for the state (Koch 1951a, 1954a). His efforts were exemplary in analyzing the bryological work conducted in California during the previous 70 years. During the 1970's through the 1990's, several moss floras based on county or other administrative units within California were developed as products of master's theses (Holmberg 1969; Jamieson 1969; Smith 1970; Spjut 1971; Strid 1974; Sigal 1975; McGrew 1976; Toren 1977; Long 1978; Mishler 1978; Harpel 1980a; Bourell 1981; Showers 1982; and Yurky 1990). These studies added new records for the state and contributed additional distribution and habitat information, including one species new to science (Showers 1980). An excellent overview of the history of California bryology was provided by Thiers and Emory (1992).

FUTURE OF BRYOLOGY IN CALIFORNIA

A variety of bryologists and plant enthusiasts continue to collect mosses in California. The senior author has made over 35,000 bryophyte collections in the state in the pursuit of writing a moss flora for California. These collections account for the majority of the new additions to the California moss flora made since the work of Koch (1950a). Additional moss records for California have resulted from bryological collecting by the junior author primarily in the central and southern Sierra Nevada. Large portions of California still need to be systematically collected by bryologists, especially the Great Basin, Desert Mojave and Desert Sonoran geographic subdivisions (Hickman 1993). During the field and herbarium work for this catalogue we

have determined that several moss species are new to science. Genera with undescribed Californian species include *Atrichum*, *Bryum*, *Homalothecium*, *Orthodicranum*, *Orthotrichum*, *Ptychomitrium*, *Schistidium*, *Syntrichia* and *Tortula*. These new taxa will be officially published in journals by us and other collaborators. Besides taxa that we have concluded are new to science, we also encountered many collections that we were not able to identify with a high level of confidence. Future work for monographers, especially within the Pottiaceae, will find much yet to discover within the collections residing in California herbaria. We are also convinced that noteworthy range extensions and mosses new for California remain to be documented.

The level of interest in California mosses is increasing. Various conservation groups concerned with the preservation of plant diversity are now beginning to include cryptogams in field surveys and in habitat conservation plans. For the first time, bryophytes are included in the 6th edition of the California Native Plant Society's *Inventory of rare and endangered plants of California* (CNPS 2001) and as a new component of the California Natural Diversity Database operated by the California Department of Fish and Game. Land management agencies are beginning to recognize and understand the important role bryophytes play in ecosystem function. This awareness is also creating the need for more field bryologists with collection and identification skills. The need for such bryological studies and training continues but few universities today consider floristic or bryogeographical studies to be appropriate for master's or doctoral degrees. The lack of professors trained in floristic botany further handicaps graduate students who wish to pursue these avenues of research, inquiry, or professional botanical employment. Nonetheless, bryology is a field where one can begin to explore without formal educational opportunities, especially if other mentors can be available to assist the budding bryologist. Schofield (1985), Malcolm and Malcolm (2000), Shaw and Goffinet (2000), and Crum (2001) are the four essential bryological works that will provide a foundation for the study of bryophytes. Lawton (1971) and Flowers (1973) are the two primary moss floras useful for the study of California mosses.

Bryological interest in California is currently centered in the northwestern portion of the state as a requirement to implement the Northwest Forest Plan. This federal land-use plan spanning three states (California, Oregon, and Washington) within the range of the northern spotted owl directs various surveys for cryptogams thought to be either rare or with undetermined viability. Many of these taxa are presumed to be restricted to late successional forest habitats. Efforts are now under way to expand the conservation of bryophytes first identified in the Sierra Nevada Ecosystem Project (Shevock 1996) and the subsequent plan amendment pro-

cess outlined in the Sierra Framework to update the 10 national forest land and resource management plans within the Sierra Nevada. The focus of bryological interest in the Sierra Nevada is centered on the conservation and management of fen habitats. Fens in the Sierra Nevada comprise about two percent of the land base yet they contain a high percentage of the species documented for this mountain range. It is again government interests, much as it was during the period of land surveys and expeditions of the 1800's to inventory the western United States (Slack 1993), that are providing the current career opportunities for taxonomic and conservation oriented botanists and bryologists.

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APPENDIX I

CATALOGUE OF CALIFORNIA MOSSES

Mosses preceded by an asterisk (*) denote those taxa that have not been previously reported in the bryological literature as occurring in California. The codes for the geographic subdivisions are provided in Figure 1. The number of specimens cited is not an indication of rarity or commonness except when fewer than five collections have been found.

Acaulon rufescens A. Jaeger [Pottiaceae]

Literature: Shevock and Toren 2001. As *Acaulon muticum* Howe 1896; Kellman 2003; Koch 1950a; Toren 1977; Yurky 1995. As *Acaulon muticum* var. *rufescens* Crum and Anderson 1981. As *Sphaerangium muticum* Brandegees 1891; Lesquereux 1868; Lesquereux and James 1884; Watson 1880.
Illustrations: Crum and Anderson 1981; Smith 1978. As *Acaulon muticum* Ignatov and Ignatova 2003.
Geographic subdivisions: CaR, CW, GV, NW, SN.
Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris* 87165; Humboldt Co.: Highway 36 about 2 miles east of Carlotta, *Norris* 48206; Lake Co.: Indian Valley Lake near dam, *Norris* 67538; Monterey Co.: cemetery on Lockwood Road east of Alamo Air Strip, Hunter-Liggett Military Reservation, *Norris* 87322; Santa Barbara Co.: El Capitan State Beach west of Santa Barbara, *Norris* 68146; Sierra Co.: near Alleghany about 4 miles from Highway 49, Tahoe National Forest, *Norris* 67413; Trinity Co.: Trinity River about 4 miles east of Del Loma, Shasta-Trinity National Forest, *Norris* 72793.

**Acaulon triquetrum* (Spruce) C. Müller Hal. [Pottiaceae]

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Smith 1978; Zander 1993.
Geographic subdivisions: CW, DSon, SW.
Selected specimens: San Diego Co.: canyon above Bow Willow Canyon Campground, Anza Borrego State Park, *Norris* 77711 & 77720 (confirmed by Zander); San Luis Obispo Co.: Tower Road near west edge of Camp Roberts Military Reservation, *Norris* 100879.

Aloina ambigua (Bruch & W. P. Schimper) Limpricht [Pottiaceae]

Literature: Steere 1954; Steere et al. 1954. As *Aloina aloides* Kellman 2003. As *Aloina aloides* var. *ambigua* Harthill et al. 1979; Koch 1950a; McCleary 1972. As *Tortula ericaefolia* Howe 1897; Millspaugh and Nuttall 1923.
Illustrations: Delgadillo 1975; Sharp et al. 1994; Smith 1978; Zander 1993.
Geographic subdivisions: CaR, CW, DSon, NW, SN, SW.
Selected specimens: Contra Costa Co.: Pine Canyon near Castle Rocks, Mt. Diablo State Park, *Norris* 100785; Imperial Co.: about 2 miles east of Mountain Springs County Park, *Norris* & Piippo 82084; Kern Co.: Rancheria Road about 2 miles from Kern River, *Shevock* 12846; Lake Co.: Chalk Mountain, North Fork of Cache Creek, *Toren* 7300 (CAS); Santa Barbara Co.: La Jolla Vieja Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock* & *Rodriguez* 20873 (determined by Delgadillo); Trinity Co.: Highway 299 about 3 miles west of Big Bar, Shasta-Trinity National Forest, *Norris* 67557; Tulare Co.: Elk Creek below Potwisha Campground, Sequoia National Park, *Norris*, *Shevock*, & *Barahona* 87575.

Aloina bifrons (De Notaris) Delgadillo [Pottiaceae]

Literature: As *Aloina pilifera* Flowers 1973; Harpel 1980a; Harthill et al. 1979; Lawton 1971; McCleary 1972. As *Aloina rigida* var. *pilifera* Koch 1949a; Steere 1954.
Illustrations: Delgadillo 1975; Flowers 1973; Lawton 1971; Zander 1993.
Geographic subdivisions: CW, DMoj, DSon, GV, SN, SW.
Selected specimens: Fresno Co.: Highway 198 about 4 miles east of Coalinga, *Norris* 68051; Kern Co.: Hart Park northeast of Bakersfield, *Shevock* 12841; Lassen Co.: Amedee Canyon of Honey Lake, *Norris* 80994; Los Angeles Co.: Highway 138 about 3 miles west of Palmdale, *Norris* 68092; Riverside Co.: South Fork San Jacinto River about 7 miles east of Hemet, *Norris* 58045 and Rouse Ridge Road, San Jacinto Mountains, *Harpel* 171 (pers. herb.); San Luis Obispo Co.: Highway 58 about 1 mile east of La Panza Ranch, Los Padres National Forest, *Norris* 76287.

***Aloina rigida* (Hedwig) Limpricht [Pottiaceae]**

Literature: Harthill et al. 1979; Kellman 2003; Koch 1950a; Lawton 1971; Mishler 1978; Sayre 1940.

Illustrations: Crum and Anderson 1981; Delgadillo 1975; Ignatov and Ignatova 2003; Lawton 1971; Sharp et al. 1994; Smith 1978; Zander 1993.

Geographic subdivisions: CW, GV, SN, SW.

Selected specimens: Fresno Co.: Warthan Creek about 7 miles from Coalinga, *Norris* 55133; Madera Co.: County Road 29 near Eastman Lake, *Shevock* 14915; Monterey Co.: School Hill, Francis Simes Hastings Reservation, *Linsdale* 301 (UC); Riverside Co.: Santa Margarita Ecological Reserve, SDSU, *Kellman* 1279b (CAS); San Luis Obispo Co.: Highway 58 about 1 mile east of La Panza Ranch, *Norris* 76284; Santa Clara Co.: Alum Rock Park, San Jose, *Steere & Sharp s.n.* (UC); Santa Cruz Co.: near China Grade Road and Highway 236, Big Basin Redwoods State Park, *Kellman* 1307 (CAS).

***Alsia californica* (W. J. Hooker & Arnott)**

Sullivant [Leptodontaceae]

Literature: Bradshaw 1926; Brandegees 1891; Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Manuel 1974; McCleary 1972; Millspaugh and Nuttall 1923; Sayre 1940; Shevock and Toren 2001; Steere 1954; Sullivant 1856; Thomson and Ketchledge 1958; Watson 1880; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Alsia californica* var. *flagellifera* Renauld and Cardot 1889.

Illustrations: Brotherus 1924–1925; Lawton 1971; Manuel 1974; Sharp et al. 1994.

Geographic subdivisions: CaR, CW, NW, SW.

Selected specimens: Humboldt Co.: Dry Lagoon State Park, *Norris* 46053; Lake Co.: Hidden Valley at Hartman Creek north of Middletown, *Toren & Dearing* 5195 (CAS); Monterey Co.: Highway 1, about 10 miles south of Lucia, Los Padres National Forest, *R. & I. Duell* 1836 (UC); San Luis Obispo Co.: Highway 1 north of Moro Bay about 0.5 mile east of Cambria, *Norris* 68209; Santa Cruz Co.: Zayante Canyon Road, 4 miles south of Summit Road north of Felton, *Norris* 86871. Sonoma Co.: Austin Creek near intersection with Russian River, *Norris* 53138; Yuba Co.: north of County Road 130, 3 miles north of Challenge, *Dillingham* 989 (CAS).

***Amblystegium juratzkanum* W. P. Schimper**

[Amblystegiaceae]

Literature: Flowers 1973; Harpel 1980a; Harthill et al. 1979; Kellman 2003; Koch 1950a; Lawton 1971; Long 1978; McGrew 1976; Mishler 1978; Showers 1982; Spjut 1971; Steere et al. 1954.

Illustrations: Flowers 1973; Lawton 1971.

Geographic subdivisions: CaR, CW, MP, NW, SN, SW.

Selected specimens: Modoc Co.: north of Middle Alkali Lake northeast of Cedarville, *Norris* 47480; Mono Co.: near Mildred Lake, head of Convict Creek Trail, Inyo National Forest, *Whittemore* 1510 (CAS); Riverside Co.: Strawberry Cienega, San Jacinto Mountains, San Jacinto State Park, *Harpel* 819 (pers. herb.); Santa Clara Co.: Big Basin Way (Highway 9) about 2 miles southwest of Saratoga, *R. & I. Duell* 2170 (UC); Siskiyou Co.: Haypress Meadows, Marble Mountain Wilderness, Klamath National Forest, *Norris* 12409; Trinity Co.: trail to Packers Peak from Big Flat, Shasta-Trinity National Forest, *Norris* 8949.

***Amblystegium serpens* (Hedwig) Bruch & W. P. Schimper** [Amblystegiaceae]

Literature: Harpel 1980a; Harthill et al. 1979; Kellman 2003; Kingman 1912; Koch 1950a, 1951e, 1958; Lawton 1971; Long 1978; Shevock and Toren 2001; Showers 1982; Spjut 1971; Strid 1974; Toren 1977. As *Hypnum serpens* Lesquereux 1868; Sullivant 1856; Watson 1880.

Illustrations: Buck 1998; Flowers 1973; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, CW, MP, NW, SN, SNE, SW.

Selected specimens: Los Angeles Co.: Devils Punchbowl Canyon, San Gabriel Mountains, Angeles National Forest, *Harpel* 582 (pers. herb.); Monterey Co.: Arroyo Seco, *Norris* 48517; San Francisco Co.: Golden Gate Park, *Koch* 1635 (UC) and *Norris & Shevock* 97033; Tulare Co.: Cedar Creek, South Fork Kaweah River, Sequoia National Park, *Showers* 3273 (SFSU) and Kern Plateau off of Sirretta Pass Trail above Big Meadows, Sequoia National Forest, *Shevock & Ng* 17553.

***Amblystegium varium* (Hedwig) Lindberg**

[Amblystegiaceae]

Literature: Flowers 1973; Harthill et al. 1979; Kingman 1912; Koch 1950a; Mishler 1978; Toren 1977. As *Orthotheciella varia* Kellman 2003; Ochrya 1998a.

Illustrations: Flowers 1973; Hedenäs 2003; Ireland 1982; Sharp et al. 1994.

Geographic subdivisions: CW, DMoj, SN, SW.

Selected specimens: Kern Co.: Kern Plateau, Caldwell Creek near Kernville, Sequoia National Forest, *Laeger* 310 (CAS) and BLM Short Canyon ACEC west of Highway 14, *Laeger & Davis* 1290 (CAS) [determined by Hedenäs]; Mariposa Co.: in stream below Highway 49 about 3.3 miles southeast of Mariposa, *Shevock* 15238; San Bernardino Co.: East Fork Mountain Home Creek, San Bernardino Mountains, San Bernardino National Forest, *Wheeler* 8231 (CAS, UC); Santa Cruz Co.: along San Lorenzo River, Ben Lomond, *Kellman* 1477 (CAS); Tulare Co.: South Creek at South Creek Falls, Sequoia National Forest, *Norris* 87081.

***Amphidium californicum* (Hampe ex C. Müller Hal.) Brotherus** [Rhabdoweisiaceae]

Literature: Bourell 1981; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Koch 1950a, 1951e; Lawton 1971; Long 1978; Spjut 1971; Strid 1974; Toren 1977; Yurky 1995. As *Anoetangium californicum* Howe 1897. As *Amphoridium californicum* Lesquereux and James 1884; Moxley 1928. As *Zygodon californicus* Lesquereux 1868; Watson 1880.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, CW, MP, NW, SN. **Selected specimens:** Del Norte Co.: Smith River, Jedediah Smith Redwoods State Park, *Norris* 67327; Modoc Co.: near Mayfield Ice Caves (Siskiyou Co.), *Norris* & *Hermann* 22157; Siskiyou Co.: Upper Cliff Lakes, Klamath National Forest, *Norris* 53007; Sonoma Co.: The Cedars north of Cazadero, *Ertter & Raiche* 12859 (UC); Tulare Co.: Potwisha Campground, Marble Fork Kaweah River, Sequoia National Park, *Shevock* 12976.

***Amphidium lapponicum* (Hedwig) W. P. Schimper** [Rhabdoweisiaceae]

Literature: Flowers 1973; Holmberg 1969; Koch 1950a, 1958; Koch and Ikenberry 1954; Lawton 1971; McGrew 1976; Showers 1982. As *Zygodon lapponicus* Lesquereux 1868; Spjut 1971; Watson 1880.

Illustrations: Abramov and Volkova 1998; Flowers 1973; Ignatov and Ignatova 2003; Ignatov and Lewinsky-Haapasaari 1994; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Del Norte Co.: Little Sanger Peak, Siskiyou National Forest, *Norris* 70874; Lake Co.: west of Forest Road M-3 at Low Gap near Sheetiron Mountain, Mendocino National Forest, *Shevock, Bourell, & Toren* 15867; Mono Co.: Barney Lake, Toiyabe National Forest, *Norris* 67090; Siskiyou Co.: trail to Long Gulch Lake southwest of Callahan, Klamath National Forest, *Norris* 57522; Tehama Co.: Gurnsey Creek east of Mineral, Plumas National Forest, *Norris* 48113; Tulare Co.: General's Highway west of Clover Creek, Sequoia National Park, *Shevock & Tseng* 15755.

****Amphidium mougeotii* (Bruch & W. P. Schimper) Schimper** [Rhabdoweisiaceae]

Illustrations: Abramov and Volkova 1998; Ignatov and Ignatova 2003; Ignatov and Lewinsky-Haapasaari 1994; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Del Norte Co.: near Doctor Rock, Siskiyou Wilderness, Six Rivers National Forest, *Norris* 50287; Fresno Co.: Mist Falls Trail along South Fork Kings River, Kings Canyon National Park, *Shevock & York* 14492; Plumas Co.: about 2 miles below Cresta Power Station, *Norris* 52628; Siskiyou Co.: Duck Lake Trail near Parrot's

Mill Road, Klamath National Forest, *Norris* 22866; Tuolumne Co.: Stanislaus River at Board Mill near Sourgrass Campground, Stanislaus National Forest, *Norris* 77159.

***Anacolia baueri* Hampe** [Bartramiaceae]

Literature: Moxley 1928. As *Anacolia menziesii* var. *baueri* Koch 1950a; Lawton 1971; McCleary 1972; Toren 1977.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, CW, DMoj, NW, SN, SW.

Selected specimens: El Dorado Co.: Rock Creek Road about 4.5 miles east of Highway 193, Eldorado National Forest, *Norris & Piippo* 82290; Glenn Co.: along Ivory Mill Road west of town of Elk Creek, Mendocino National Forest, *Shevock* 15796; Los Angeles Co.: Highway 138 about 3 miles west of Palmdale, *Norris* 68093; Mariposa Co.: Merced River near South Fork, Sierra National Forest, *Norris* 69812; Santa Barbara Co.: Torrey Pine Forest, Santa Rosa Island, Channel Islands National Park, *Shevock & Norris* 20789; Siskiyou Co.: Klamath River, 1 mile west of Ash Creek Bridge, Highway 96, Klamath National Forest, *Norris* 77961; Tulare Co.: Elk Creek near Potwisha Campground, Sequoia National Park, *Shevock, Norris, & Barahona* 13192.

***Anacolia laevisphaera* (Taylor) Flowers in Grout** [Bartramiaceae]

Literature: Harthill et al. 1979.

Illustrations: Allen 2002; Sharp et al. 1994.

Geographic subdivisions: CaR, SN, SW.

Selected specimens: Butte Co.: Grubb Road about 3 miles east of Palermo, *Norris* 73582; Fresno Co.: Tollhouse Rock along Tollhouse Road, Sierra National Forest, *Shevock & York* 12715; San Diego Co.: near Campo, *Haring* 423 (UC); Tulare Co.: Marble Falls trail above Potwisha Campground, Sequoia National Park, *Shevock* 12973.

***Anacolia menziesii* (Turner) Paris** [Bartramiaceae]

Literature: Bourell 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Kingman 1912; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Long 1978; Mishler 1978; Sayre 1940; Shevock and Toren 2001; Showers 1982; Sigal 1975; Spjut 1971; Steere 1954; Steere et al. 1954; Strid 1974; Toren 1977; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Anacolia aristifolia* Cooke 1941. As *Bartramia menziesii* Bradshaw 1926; Lesquereux 1868; Watson 1880.

Illustrations: Flowers 1973; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: CaR, CW, DMoj, DSon, NW, SN, SW.

Selected specimens: Fresno Co.: Highway 180 at Horseshoe Bend above the Kings River, Sequoia National Forest, *Shevock & York* 12324a; Los An-

geles Co.: slopes of Orizaba Mountain, Santa Catalina Island, *Shevock & Thorne 4033*; Riverside Co.: between Key Ranch and Barker Dam, Joshua Tree National Park, *Norris 50538*; San Francisco Co.: Castro and 30th Streets, San Francisco, *Toren 8020* (CAS); Siskiyou Co.: Salmon River at Nordheimer Creek, Klamath National Forest, *Norris & Hermann 22768*; Tuolumne Co.: slopes of Pilot Ridge, South Fork Tuolumne River, Stanislaus National Forest, *Shevock & Haas 13427*.

****Andraea alpestris* (Thedenius) W. P. Schimper** [Andreaeaceae]

Illustrations: Murray 1988.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Del Norte Co.: Whiskey Lake, Six Rivers National Forest, *Norris 83366*; Inyo Co.: Treasure Lake west of Big Pine, John Muir Wilderness, Inyo National Forest, *Norris 46974 & 46975*; Siskiyou Co.: trail to Long Gulch Lake southwest of Callahan, Klamath National Forest, *Norris 57543* (confirmed by Murray) and McCloud River about 5 miles east of McCloud, Shasta-Trinity National Forest, *Norris & Hillyard 103919*.

***Andraea blyttii* W. P. Schimper** [Andreaeaceae]

Literature: Jessup 2000; Koch 1950a; Lawton 1971.

Illustrations: Lawton 1971; Murray 1988.

Geographic subdivisions: CaR, NW.

Selected specimens: Siskiyou Co.: about 1 mile west of Elk Lick, Klamath National Forest, *Norris 23231* and McCloud River about 5 miles east of McCloud, Shasta-Trinity National Forest, *Norris & Hillyard 103916*; Tehama Co.: Mill Creek about 0.5 mile beyond Mill Creek Campground, *Norris 55915*.

****Andraea heinemannii* Hampe & C. Müller Hal.** [Andreaeaceae]

Illustrations: Murray 1987b.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Calaveras Co.: North Fork Mokelumne River west of Moore Creek, Stanislaus National Forest, *Shevock 21742* (determined by Murray); Lake Co.: Boggs Mountain State Forest, *Showers 1810* (SFUSU) and Cobb Mountain, *Toren & Dearing 7114* (CAS) [determined by Murray]; Madera Co.: above Whiskey Creek Falls, Sierra National Forest, *Shevock, Norris, & Beyer 20237*; Marin Co.: East Peak, Mt. Tamalpais State Park, *Robertson 1728* (UC); Mariposa Co.: Highway 41 below Wawona Tunnel, Yosemite National Park, *Shevock & Norris 20178*; Shasta Co.: Castle Lake at Castle Lake Creek southwest of Mt. Shasta City, Shasta-Trinity National Forest, *Norris & Hillyard 103852*; Siskiyou Co.: McCloud River, 5 miles east of McCloud, Shasta-Trinity National Forest, *Norris & Hillyard 103898*; Tehama Co.: Highway 36 at milespost 96, *Norris 55953*; Tulare Co.: Lloyd

Meadows Basin, Sequoia National Forest, *Shevock 14259* (confirmed by Murray).

***Andraea nivalis* W. J. Hooker** [Andreaeaceae]

Literature: Showers 1982.

Illustrations: Ignatov and Ignatova 2003; Lawton 1971; Murray 1988; Smith 1978.

Geographic subdivisions: CaR.

Selected specimens: Shasta Co.: Redding Peak near Cliff Lake, Lassen Volcanic National Park, *Showers 3580* (UC) [confirmed by Murray].

***Andraea rothii* Weber & D. Mohr** [Andreaeaceae]

Literature: Lawton 1971.

Illustrations: Abramov and Volkova 1998; Ireland 1982; Lawton 1971; Murray 1988; Smith 1978.

Geographic subdivisions: NW.

Selected specimens: Lake Co.: east slope of Cobb Mountain, *Toren & Dearing 7115 & 7116* (CAS) [determined by Murray]; Siskiyou Co.: one mile east of Copper Butte, Klamath National Forest, *Norris 50250* (determined by Murray).

***Andraea rupestris* Hedwig** [Andreaeaceae]

Literature: Jessup 2000; Koch 1950a; Showers 1982; Toren 1977.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Murray 1988; Sharp et al. 1994.

Geographic subdivisions: CaR, MP, NW, SN, SNE.

Selected specimens: Amador Co.: above Kirkwood Lake east of Kirkwood, Eldorado National Forest, *Norris 82728*; Fresno Co.: slopes above Lower Twin Lake, Kaiser Wilderness, Sierra National Forest, *Shevock, Ertter, & Laeger 22857* (confirmed by Murray); Humboldt Co.: headwaters of Oregon Creek north of Trinity Summit Guard Station, Six Rivers National Forest, *Norris & Creek 50092*; Inyo Co.: above Treasure Lake west of Big Pine, John Muir Wilderness, Inyo National Forest, *Norris 46979*; Modoc Co.: Alcohol Crater Rim, Modoc National Forest, *Harpel 16324* (pers. herb.); Shasta Co.: Hot Springs Creek above Devil's Kitchen, Lassen Volcanic National Park, *Showers 2398* (UC); Siskiyou Co.: Long Gulch Lake southwest of Callahan, Klamath National Forest, *Norris 57500 & 57534* (confirmed by Murray).

***Andraea schofieldiana* B. M. Murray** [Andreaeaceae]

Literature: Christy and Wagner 1996.

Illustrations: Murray 1987a.

Geographic subdivisions: CaR, NW.

Selected specimens: Del Norte Co.: Whiskey Lake, Six Rivers National Forest, *Norris 57721 & 83378*; Siskiyou Co.: about 1 mile west of Elk Lick, Klamath National Forest, *Norris 23220* (confirmed by Murray).

***Anomobryum julaceum* (Schrader ex P. G. Gärtner, B. Meyer & Scherbius) W. P. Schimper** [Bryaceae]

Literature: Kellman 2003. As *Anomobryum filiforme* Koch 1950a. As *Pohlia filiformis* Lawton 1971.

Illustrations: Allen 2002; Crum and Anderson 1981; Ireland 1982; Lawton 1971.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Contra Costa Co.: Mt. Diablo State Park, *Norris 100541*; Humboldt Co.: road to Petrolia, 0.5 mile above Ferndale, *Peterson 206* (UC) and Highway 96 near Skunk Creek about 3 miles south of Weitchpec, *Norris 58309*; Mariposa Co.: Yosemite Falls, Yosemite National Park, *Koch 1685* (Koch 1950a); Santa Cruz Co.: Quail Hollow Ranch County Park, *Kellman 193* (UC) & *948* (CAS) [confirmed by Spence]; Big Basin Redwoods State Park, *Schofield 29129* (UC) [determined by Shaw], Empire Grade about 0.5 mile uphill from Smith Grade, *Kellman 1455* (CAS) and near China Grade Road and Highway 236, Big Basin Redwoods State Park, *Kellman 1314* (CAS); Shasta Co.: Clear Creek below Clear Creek Bridge, *Shevock, Toren, & Dearing 23874* and near Whiskeytown Environmental Camp, Whiskeytown National Recreation Area, *Shevock & Toren 23888*; Sonoma Co.: Calistoga Road near intersection with St. Helena Road about 3 miles north of Highway 12 near Santa Rosa, *Robertson 531* (CAS).

***Antitrichia californica* Sullivant in Lesquereux** [Leucodontaceae]

Literature: Bourell 1981; Bradshaw 1926; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Kingman 1912; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Long 1978; McCleary 1972; Millsbaugh and Nuttall 1923; Mishler 1978; Sayre 1940; Shevock and Toren 2001; Showers 1982; Spjut 1971; Steere 1954; Thomson and Ketchledge 1958; Toren 1977; Watson 1880; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Antitrichia californica* var. *ambigua* Renauld and Cardot 1890.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, CW, MP, NW, SN, SW.

Selected specimens: Lake Co.: Clear Lake State Park, *Norris 47721*; Modoc Co.: Boles Creek southeast of Clear Lake, *Norris 79170*; Monterey Co.: Nacimiento-Ferguson Road at boundary of Hunter-Liggett Military Reservation, *Norris 87344*; Orange Co.: Silverado Canyon, Cleveland National Forest, *Shevock 3995*; Shasta Co.: Fall Creek Road at Dekkas Rock above Lake Shasta, Shasta-Trinity National Forest, *Norris 84814*; Tulare Co.: Wishon Fork Tule River above Wishon Campground, Sequoia National Forest, *Shevock & Morosco 16802*.

***Antitrichia gigantea* (Renauld & Cardot) Kindberg** [Leucodontaceae]

Literature: As *Antitrichia curtispindula* Christy and Wagner 1996; Harthill et al. 1979; Holmberg

1969; Jamieson 1969; Koch 1950a; Lawton 1971; Lesquereux 1868; Long 1978; Sullivant 1856; Thomson and Ketchledge 1958. As *Antitrichia curtispindula* var. *gigantea* Lesquereux 1868; Watson 1880.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Lawton 1971; Schofield 1969b.

Geographic subdivisions: CaR, CW, NW.

Selected specimens: Del Norte Co.: French Hill Road about 3.5 miles above Highway 199 southwest of Gasquet, Six Rivers National Forest, *Norris 85058*; Humboldt Co.: East Fork about 5 air miles north of Mad River, Six Rivers National Forest, *Norris 83891*; Mendocino Co.: Mill Creek County Park Recreational Area about 8 miles east of Ukiah, *Norris 72636*; and Hopland, *Layne s.n.* (UC); San Mateo Co.: Butano Fire Trail, Butano State Park, *Becking 910614* (UC); Siskiyou Co.: Doe Creek, *Norris 23077* and McCloud River Preserve, The Nature Conservancy, *Norris & Hillyard 106581*; Trinity Co.: Canyon Creek between Ripstein Camp and McKay Camp, *Norris 8001*.

***Archidium alternifolium* (Dickson ex Hedwig) Mitten** [Archidiaceae]

Literature: Kellman 2003. The historic California collections cited in the bryological literature as *Archidium alternifolium* we have determined to represent *Pleuroidium subulatum*. This species, however, was recently confirmed for the state.

Illustrations: Grout 1928–1940; Ignatov and Ignatova 2003; Snider 1975.

Geographic subdivisions: CW.

Selected specimens: Santa Cruz Co.: Headwaters of Pleasley Gulch near Wilder Ridge Loop Trail, Wilder Ranch State Park, *Kellman 2249* (CAS) [confirmed by Spence].

***Arctoa fulvella* (Dickson) Bruch & W. P. Schimper** [Dicranaceae]

Literature: McGrew 1976.

Illustrations: Crum and Anderson 1981; Smith 1978.

Geographic subdivisions: CaR, NW.

Selected specimens: Siskiyou Co.: Russian Lake, Klamath National Forest, *McGrew 378* (UC), Little Grayback, near Indian Creek, *Holmberg 921* (UC), Granite Creek between Tickner Creek and Blue Granite Lake, Klamath National Forest, *Norris 52325*, Sawtooth Ridge at crest of Caribou Rim along trail from Big Flat to Caribou Basin, Klamath National Forest, *Norris 9211*; Trinity Co.: crest of ridge above East Weaver Lake, *Norris 9374*.

***Atractylorcarpus flagellaceus* (C. Müller Hal.) Williams** [Dicranaceae]

Literature: Shevock 2000. [See also Frahm & Isoviita 1988.]

Illustrations: Sharp et al. 1994.

Geographic subdivisions: CaR, NW.

Selected specimens: Butte Co.: Upper Bidwell

Park between Big Chico Creek and Sycamore Creek, *Janeway 6986* (UC); Trinity Co.: Highway 299 about 0.25 mile from road junction to Helena, Shasta-Trinity National Forest, *Shevock, Lin, & Chen 17741* (determined by J-P Frahm) and *Norris 99803*; Highway 299 near Whites Bar Creek west of Big Bar, *Norris 68431*.

***Atrichum selwynii* Austin** [Polytrichaceae]

Literature: Bourell 1981; Holmberg 1969; Jamieson 1969; Kellman 2003; Lawton 1971; Smith 1970; Spjut 1971; Stark and Whittemore 1992; Toren 1977; Yurky 1990.

Illustrations: Flowers 1973; Frye 1949; Lawton 1971; Nyholm 1971.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Contra Costa Co.: Mt. Diablo State Park, *Norris 100482*; Humboldt Co.: Tolkan Recreation Area east of Shelter Cove, *Norris 23469*; Mariposa Co.: near Crane Flat Meadow, Yosemite National Park, *Kellman 548* (CAS); Placer Co.: Drum Forebay Road about 1 mile north of Highway 80, Tahoe National Forest, *Norris 81987*; Santa Clara Co.: Highway 9 about 2 miles from Saratoga, *R. & I. Duell 2178* (UC); Trinity Co.: Highway 36 about 4 miles west of Forest Glen, *Norris 23849*.

***Atrichum undulatum* (Hedwig) Palisot de Beauvois** [Polytrichaceae]

Literature: Brandegees 1891; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lesquereux 1868; Steere et al. 1954; Yurky 1990, 1995. As *Catharinea callibryon* Watson 1880. As *Catharinea undulata* Bradshaw 1926.

Illustrations: Abramov and Volkova 1998; Ignatov and Ignatova 2003; Ignatov and Smith Merrill 1995; Ireland 1982; Nyholm 1971; Smith 1978.

Geographic subdivisions: CW, NW, SN.

Selected specimens: Calaveras Co.: Moran Creek 1 mile north of Avery, *Wagner 4360* (UC); Sonoma Co.: Guerneville, *Cook 244* (UC); Santa Cruz Co.: Quail Hollow Ranch, *Kellman 300* (CAS) and Last Chance Road near Last Chance Creek, *Kellman 896* (CAS).

***Aulacomnium androgynum* (Hedwig) Schwägrichen** [Aulacomniaceae]

Literature: Bradshaw 1926; Bourell 1981; Cooke 1941; Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Kellman 2003; Kingman 1912; Koch 1949a, 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Long 1978; McGrew 1976; Shevock and Toren 2001; Showers 1982; Sigal 1975; Smith 1970; Spjut 1971; Steere et al. 1954; Sullivant 1856; Thomson and Ketchledge 1958; Toren 1977; Watson 1880; Yurky 1990, 1995.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, CW, MP, NW, SN, SNE, SW.

Selected specimens: Kern Co.: Greenhorn Mountains near Greenhorn Summit, Sequoia National Forest, *Shevock 15096*; Lake Co.: Upper Nye Campground, Snow Mountain, Mendocino National Forest, *Shevock, Bourell, & Toren 15851*; Modoc Co.: Joseph Creek, Warner Mountains, Modoc National Forest, *Sanger s.n.* (UC); Riverside Co.: Indian Creek, James Reserve, San Jacinto Mountains, *Harpel 1399* (pers. herb.); Santa Clara Co.: Abohe Creek above Hidden Villa Ranch, *Herre & Wiggins 27* (UC); San Diego Co.: confluence of Doane and French Creek, Palomar Mountains, *Stark 546* (MO); Siskiyou Co.: Elk Creek at Malone Creek south of Happy Camp, Klamath National Forest, *Norris 52231*.

***Aulacomnium palustre* (Hedwig) Schwägrichen** [Aulacomniaceae]

Literature: Flowers 1973; Harthill et al. 1979; Kellman 2003; Koch 1949a, 1950a, 1958; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; McCleary 1972; McGrew 1976; Showers 1982; Spjut 1971; Watson 1880.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, MP, NW, SN, SNE.

Selected specimens: Butte Co.: Jonesville, *Cope-land 1551* (UC); Humboldt Co.: Bald Mountain between High Prairie and Snow Camp, *Tracy 4600* (UC); Lake Co.: north cirque of Hull Mountain, Mendocino National Forest, *Toren & Dearing 7228* (CAS); Mono Co.: Mormon Meadow, Cinnabar Canyon off of Highway 270, 3 miles east of Highway 395 on road to Bodie, *Shevock 15341*; Siskiyou Co.: near Monument Lake, Marble Mountain Wilderness, Klamath National Forest, *Norris & Spjut 12434*; Tulare Co.: Mosquito Lakes, Mineral King, Sequoia National Park, *Shevock & O'Brien 15965*.

***Barbula convoluta* Hedwig** [Pottiaceae]

Literature: Brandegees 1891; Crum and Anderson 1981; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Mishler 1978; Shevock and Toren 2001; Showers 1982; Spjut 1971; Steere 1954; Steere et al. 1954; Sullivant 1856; Toren 1977; Watson 1880; Zander 1997.

Illustrations: Abramov and Volkova 1998; Allen 2002; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Saito 1975; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, DMoj, DSon, GV, NW, SN, SW.

Selected specimens: Fresno Co.: Auberry, *Ikenberry 1020* (MO) [determined by Koch; Zander]; Humboldt Co.: False Klamath Cove, Redwood Na-

tional Park, *Norris* 48302; Inyo Co.: mouth of Cottonwood Canyon, Death Valley National Park, *Kellman, Shevock, York, & Knaus* 1415a (CAS) [determined by Stark]; Monterey Co.: Hastings Reservation, *Linsdale* 41-45 (UC) and Pacific Grove, *Heller* 6485 (MO); Riverside Co.: Devils Slide Trail, San Jacinto Mountains, San Bernardino National Forest, *Harpel* 949 (pers. herb.); San Francisco Co.: De Laveaga Dell, Aids Memorial Grove, Golden Gate Park, *Shevock* 19517 and Twin Peaks, *Eastwood* 57 (MO) [determined by Zander]; Shasta Co.: Millville Plains Road about 6 miles east of Anderson, *Norris* 23695; Sutter Co.: Philip Road near junction with Fiddymont Road northwest of Roseville, *Norris* 103783; Tulare Co.: Pixley Vernal Pools Preserve, San Joaquin Valley, *McClintock* s.n. (CAS, UC).

****Barbula ehrenbergii* (Lorentz) Fleischer**
[Pottiaceae]

Illustrations: Flowers 1973.

Geographic subdivisions: SNE.

Selected specimens: Mono Co.: Convict Lake Trail near trail junction to Lake Genevieve, John Muir Wilderness, Inyo National Forest, *Shevock & York* 20011.

****Barbula eustegia* Cardot & Thériot**
[Pottiaceae]

Illustrations: Flowers 1973; Lawton 1971.

Geographic subdivisions: CW, GV.

Selected specimens: Contra Costa Co.: Mitchell Canyon, Mt. Diablo State Park, *Norris* 100603; Shasta Co.: Highway turnoff for Shasta College north of Redding, *Norris* 56653 & 57784.

***Barbula unguiculata* Hedwig** [Pottiaceae]

Literature: Harpel 1980a; Harthill et al. 1979; Kellman 2003; Koch 1950a; Shevock and Toren 2001.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Saito 1975; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, DMoj, NW, SW.

Selected specimens: Butte Co.: Grubb Road about 3 miles east of Palermo, *Norris* 73596; Los Angeles Co.: Ferndale, *MacFadden* 22740 (MO) [determined by Zander]; Lake Co.: Library Park, Lakeport, *Toren* 7663 (CAS); Mendocino Co.: Pygmy Forest about 5 miles east of Albion, *Norris* 11784; Orange Co.: Walker Lee Drive, Rossmoor, *Norris* 57806; Riverside Co.: Carrizo Creek, Santa Rosa Mountains, *Harpel* 1392 (pers. herb.); San Francisco Co.: Presidio of San Francisco, *Shevock* 19360; Ventura Co.: Upper North Fork Matilija Creek, Matilija Wilderness, Los Padres National Forest, *Shevock* 12556.

***Bartramia ithyphylla* Bridel** [Bartramiaceae]

Literature: Crum and Anderson 1981; Flowers 1973; Koch 1950a, 1958; Lawton 1971; Lesquer-

eux 1868; McGrew 1976; Showers 1982; Spjut 1971; Watson 1880.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Alpine Co.: Winnemucca Lake, Eldorado National Forest, *Norris* 71271; Fresno Co.: Taboose Pass Trail, headwaters of South Fork Kings River, Kings Canyon National Park, *Shevock* 13852; Mono Co.: Tioga Junction Campground, about 2.5 miles north of Tioga Pass on Highway 120, Inyo National Forest, *Norris* 48346; Siskiyou Co.: South Fork Lakes west of Callahan, Klamath National Forest, *Norris* 76910; Tuolumne Co.: Lower Young Lake, Yosemite National Park, *Messick* 677 (UC).

***Bartramia pomiformis* Hedwig** [Bartramiaceae]

Literature: Holmberg 1969; Spjut 1971.

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, NW.

Selected specimens: Del Norte Co.: shore of Sanger Lake, Siskiyou National Forest, *Norris* 70835, Smith River at Middle Fork Jones River, *Norris* 46235 and Smith River about 16 miles east of Gasquet on Highway 199, *Norris* 8894; Humboldt Co.: Goose Creek, *Norris* 56492; Siskiyou Co.: near Sugar & Salmon Creeks, Marble Mountains, Klamath National Forest, *Halling* 1350 (CAS, SFSU), northeast of Cook and Green Pass, Rogue River National Forest, *Shevock & Toren* 20014; Trinity Co.: Onion Lake Road about 7 miles south of Onion Lake, *Norris* 72521.

***Bartramia stricta* Bridel** [Bartramiaceae]

Literature: Brandegee 1891; Harthill et al. 1979; Howe 1897; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Long 1978; McCleary 1972; Sayre 1940; Shevock and Toren 2001; Showers 1982; Toren 1977; Watson 1880; Whittemore and Sommers 1999; Yurky 1990, 1995.

Illustrations: Lawton 1971. See also Hermann 1980.

Geographic subdivisions: CaR, CW, GV, NW, SN, SW.

Selected specimens: Humboldt Co.: Trinity River about 2 miles east of Salyer, Shasta-Trinity National Forest, *Norris* 67267; Lake Co.: north end of Bachelor Valley near Hell's Peak, *Toren & Dearing* 6862 (CAS) [confirmed by Griffin III]; Nevada Co.: Slack's Ravine, Highway 20 about 7 miles west of Rough and Ready, *Norris* 67461; Riverside Co.: Santa Margarita River between Temecula and Fallbrook, SDSU Santa Margarita Ecological Reserve, *Shevock & Jessup* 20534; San Francisco Co.: Glen Canyon, *Shevock* 19185; San Luis Obispo Co.: Santa Rosa Creek about 0.5 mile east of Cambria, *Norris* 68215; Shasta Co.: Sacramento River Trail

northeast of Redding, *Norris* 105288; Tehama Co.: Highway 36 about 2 miles southwest of Dales, *Norris* 55994.

***Bestia longipes* (Sullivant & Lesquereux)**

Brotherus [Brachytheciaceae]

Literature: Harthill et al. 1979; Kellman 2003; Koch 1950a; Mishler 1978; Steere 1954; Toren 1977; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Alsia longipes* Bradshaw 1926; Kingman 1912; Lequereux 1868. Misapplied as *Bestia "brevipes"* McCleary 1972.

Illustrations: Grout 1928–1940; Sullivant 1864.

Geographic subdivisions: CaR, CW, NW, SN, SW.

Selected specimens: Alameda Co.: Strawberry Creek east of Hilgard Hall, U. C. Berkeley, *Norris* 82503; Humboldt Co.: South Fork Trinity River, *Tracy* 7371 (UC); Lake Co.: base of Mt. Konocti, Clear Lake State Park, *Toren* 6844 (CAS); Placer Co.: Clover Creek at Sierra College Road, *Norris* 81932; Santa Barbara Co.: off Highway 154 along old Stagecoach Road at Cold Springs Tavern, Los Padres National Forest, *Laeger* 526 (CAS) and Water Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock & Rodriguez* 20817; Santa Cruz Co.: Zayante Canyon Road about 4 miles south of Summit Road north of Felton, *Norris* 86869; Shasta Co.: Indian Springs, Castle Crags State Park, *Norris* 103037; Siskiyou Co.: Highway 96 about 2 miles east of Fort Goff, Klamath National Forest, *Norris* 72272.

***Blindia acuta* (Hedwig) Bruch & W. P.**

Schimper [Seligeriaceae]

Literature: Crum and Anderson 1981; Holmberg 1969; Kellman 2003; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; McGrew 1976; Showers 1982; Thomson and Ketchledge 1958.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971.

Geographic subdivisions: CaR, CW, NW, SN, SNE.

Selected specimens: Alpine Co.: Winnemucca Lake, Mokelumne Wilderness, Eldorado National Forest, *Norris* 71263; Humboldt Co.: South Fork of Tish-Tang-a-Tang Creek east of Hoopa, *Norris & Whittemore* 52413; Inyo Co.: Treasure Lake, John Muir Wilderness, Inyo National Forest, *Norris* 71529; Siskiyou Co.: South Sugar Lake, Klamath National Forest, *Norris & McGrew* 45644; Tulare Co.: Forest Road 14S11 near bridge crossing of Big Meadows Creek, Sequoia National Forest, *Shevock & York* 13677; Tuolumne Co.: near Olmstead Point, Yosemite National Park, *Kellman* 504 (CAS).

***Brachythecium albicans* (Hedwig) Bruch & W.**

P. Schimper [Brachytheciaceae]

Literature: Bradshaw 1926; Flowers 1973; Harthill et al. 1979; Holmberg 1969; Howe 1896; Ireland 1982; Kellman 2003; Koch 1950a, 1951e,

1958; Koch and Ikenberry 1954; Lawton 1971; McCleary 1972; McGrew 1976; Showers 1982; Spjut 1971; Strid 1974; Thomson and Ketchledge 1958; Toren 1977; Whittemore and Sommers 1999; Yurky 1995.

Illustrations: Abramov and Volkova 1998; Flowers 1973; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Fresno Co.: Grizzly Falls along Highway 180, South Fork Kings River, Sequoia National Forest, *Shevock* 12438; Lake Co.: Upper Nye Camp Site just north of Snow Mountain Wilderness boundary, Mendocino National Forest, *Shevock, Bourell, & Toren* 15841; San Mateo Co.: Big Canyon Park at Brittan Avenue just east of Crestview, San Carlos, *Whittemore* 4295 (UC); Trinity Co.: Hall City Caves east of Wildwood, Shasta-Trinity National Forest, *Norris* 71687.

***Brachythecium asperrimum* (C. Müller Hal.)**

Sullivant [Brachytheciaceae]

Literature: Flowers 1973; Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Shevock and Toren 2001; Spjut 1971; Toren 1977. As *Brachythecium washingtonianum* Crum 1957; Koch 1950a, 1958; Koch and Ikenberry 1954. As *Hypnum asperrimum* Watson 1880. As *Hypnum vallium* Lesquereux 1868.

Illustrations: Flowers 1973; Lawton 1971; Robinson 1962.

Geographic subdivisions: NW, SN.

Selected specimens: Fresno Co.: Cedar Grove at Cedar Creek, Kings Canyon National Park, *Shevock* 13764; Humboldt Co.: Highway 299 east of Arcata, *Norris* 55082; San Francisco Co.: Chain of Lakes, Golden Gate Park, San Francisco, *Shevock* 19163; Santa Cruz Co.: Big Basin State Park, *Schofield* 6357 (CAN) [determined by Crum]; Tulare Co.: north base of Slate Mountain, Sequoia National Forest, *Shevock* 15661.

***Brachythecium bolanderi* (Lesquereux) A.**

Jaeger [Brachytheciaceae]

Literature: Harthill et al. 1979; Howe 1896; Kellman 2003; Kingman 1912; Koch and Ikenberry 1954; Lawton 1971; Long 1978; McGrew 1976; Showers 1982; Toren 1977. As *Hypnum bolanderi* Lawton 1965b; Lesquereux 1868; Watson 1880.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, CW, MP, NW, SN.

Selected specimens: San Luis Obispo Co.: Queen Bee Campground about 1 mile from La Panza Summit, *Norris* 55184; Santa Cruz Co.: Fall Creek, Henry Cowell Redwoods State Park, *Kellman* 661 (CAS); Shasta Co.: Pit River at Potem Falls northwest of Round Mountain, *Norris* 76324; Siskiyou Co.: shores of Castle Lake southwest of Shasta City, Shasta-Trinity National Forest, *Norris* 99777, Trail Gulch Lake west of Callahan, Klamath National Forest, *Norris* 102544 and 1 mile west of Elk

Lick, Klamath National Forest, *Norris* 23206; Sonoma Co.: Duran County Park near Bodega Marine Laboratory, *Norris* 103496; Tulare Co.: slopes above Oriole Lake, Sequoia National Park, *Shevock* 17634.

****Brachythecium calcareum* Kindberg**
[Brachytheciaceae]

Illustrations: Crum and Anderson 1981.

Geographic subdivisions: NW.

Selected specimens: Siskiyou Co.: Forest Road 40S01 along Jaynes Creek to headwaters, Klamath National Forest, *Norris* 48655 and Bear Creek between junction with Elk and Snowshoe Creek, *Norris* 24166.

***Brachythecium collinum* (Schleicher ex C. Müller Hal.) Bruch & W. P. Schimper**
[Brachytheciaceae]

Literature: Flowers 1973; Harthill et al. 1979; Holmberg 1969; Howe 1896; Koch 1950a, 1951e, 1958; Lawton 1971; Long 1978; McGrew 1976; Showers 1982; Spjut 1971; Strid 1974. As *Hypnum collinum* & *H. hillebrandi* Lesquereux 1868; Watson 1880.

Illustrations: Flowers 1973; Ignatov 1998; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: DMoj, NW, SN, SNE, SW.

Selected specimens: Fresno Co.: north face of Spanish Mountain, John Muir Wilderness, Sierra National Forest, *Shevock & York* 12421; Inyo Co.: slopes of Rogers Peak, Death Valley National Park, *Shevock, York, & Davis* 21367; Lake Co.: Summit Springs Trail, Snow Mountain Wilderness, Mendocino National Forest, *Toren & Dearing* 7464 (CAS); San Bernardino Co.: Dollar Lake Trail, San Gorgonio Wilderness, San Bernardino National Forest, *Harpel* 2188 (pers. herb.); Tuolumne Co.: White Wolf, Yosemite National Park, *Kellman* 499 (CAS).

***Brachythecium erythrorrhizon* Bruch & W. P. Schimper** [Brachytheciaceae]

Literature: Jamieson 1969; Koch 1950a, 1951e; McGrew 1976; Spjut 1971.

Illustrations: Ignatov 1998; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Alpine Co.: Highway 88 at Hope Valley, Toiyabe National Forest, *Norris* 48499; Fresno Co.: Smith Meadows, Sierra National Forest, *Shevock et al.* 17458; Mariposa Co.: Summit Road two miles north of Fish Camp, Sierra National Forest, *Norris* 85360; Santa Barbara Co.: Bates Canyon, Cole Springs Campground, *Norris* 55352; Siskiyou Co.: upper Abbott's Cabin at Big Meadow, Marble Mountain Wilderness, Klamath National Forest, *Spjut* 1521 & 1523 (UC) and Big Boulder Lake west of Carrville, Klamath National Forest, *Norris & Streiman* 74844; Tehama Co.:

Tomhead Gulch, Shasta-Trinity National Forest, *Norris* 56906.

***Brachythecium fendleri* (Sullivant) A. Jaeger**
[Brachytheciaceae]

Literature: Lawton 1965b.

Illustrations: Flowers 1973; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: DMoj, NW, SN, SNE, SW.

Selected specimens: Kern Co.: Piute Mountain Road, BLM Piute Cypress Natural Area, Piute Mountains, *Shevock* 12493; Fresno Co.: Stump Springs Road near Aspen Creek, Sierra National Forest, *Norris & Shevock* 100114; Inyo Co.: slope of Rogers Peak near Hummingbird Spring, Death Valley National Park, *Shevock, York, & Davis* 21364; Mariposa Co.: Crane Flat Meadow, Yosemite National Park, *Kellman* 545 (CAS); Riverside Co.: road to Dark Canyon, San Bernardino National Forest, *Harpel* 75 (pers. herb.); Siskiyou Co.: Sugar Creek at Sugar Lake west of Callahan, Klamath National Forest, *Norris* 57302; Tulare Co.: trail to Lake South America, Sequoia National Park, *Laeger* 175 (CAS) and Moro Rock, *Shevock, Lin, & Chen* 17762; Tuolumne Co.: Haring Creek Reservoir, Stanislaus National Forest, *Norris* 100407.

***Brachythecium frigidum* (C. Müller Hal.) Bescherelle** [Brachytheciaceae]

Literature: Bourell 1981; Harpel 1980a; Harthill et al. 1979; Kellman 2003; Lawton 1971; Long 1978; Mishler 1978; Showers 1982; Strid 1974. As *Brachythecium lamprochryseum* Bradshaw 1926; Cooke 1941; Flowers 1973; Howe 1897; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; McGrew 1976; Spjut 1971.

Illustrations: Flowers 1973; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: CaR, CW, NW, SN, SNE, SW.

Selected specimens: Fresno Co.: Smith Meadow, Sierra National Forest, *Shevock & York* 13588 (determined by Ochrya); Riverside Co.: Deep Springs Trail, San Jacinto Mountains, San Bernardino National Forest, *Harpel* 549 (pers. herb.); Siskiyou Co.: Gumboot Creek, South Fork Sacramento River, Shasta-Trinity National Forest, *Norris* 99797; Tehama Co.: South Fork Beegum Creek, Shasta-Trinity National Forest, *Shevock & Ertter* 19414.

***Brachythecium holzingeri* (Grout) Grout**
[Brachytheciaceae]

Literature: McGrew 1976. We were unable to locate the McGrew packet cited in her thesis, but we determined another California collection to represent this species.

Illustrations: Lawton 1971.

Geographic subdivisions: CW.

Selected specimens: Santa Cruz Co.: Bridge Creek Trail, Forest of Nisene Marks State Park, *Kellman* 2641 (CAS).

****Brachythecium hylotapetum* N. Higinbotham & B. Higinbotham** [Brachytheciaceae]

Illustrations: Higinbotham and Higinbotham 1958; Lawton 1971.

Geographic subdivisions: NW, SNE.

Selected specimens: Humboldt Co.: near Coyote Peak on Bald Hills Road, *Norris* 22346; Mono Co.: Lower Rock Creek Trail, Inyo National Forest, *Nelson* 555 (UC).

***Brachythecium leibergii* Grout** [Brachytheciaceae]

Literature: Lawton 1965b; McGrew 1976; Showers 1982; Spjut 1971.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Del Norte Co.: Bear Basin Creek north of Bear Basin Butte, *Norris* 68862; Butte Co.: French Creek north of Brush Creek Gold Camp, Plumas National Forest, *Norris* 99485; Inyo Co.: above Chocolate Lake west of Big Pine, John Muir Wilderness, Inyo National Forest, *Norris* 46889; Siskiyou Co.: Granite Creek between Tickner Creek and Blue Granite Lake, *Norris* 52300; Trinity Co.: Hall City Caves east of Wildwood, Shasta-Trinity National Forest, *Norris* 71680 and trail above Bridge Camp west of Clair Engle Lake, *Norris* 68781; Tulare Co.: Ranger Lakes, Kings Canyon National Park, *Norris* 46549 and Summit Trail at Jacobsen Meadow, Golden Trout Wilderness, Sequoia National Forest, *Laeger* 396 (CAS).

****Brachythecium nelsonii* Grout**

[Brachytheciaceae]

Illustrations: Flowers 1973; Lawton 1971.

Geographic subdivisions: SN.

Selected specimens: Tulare Co.: South Fork Tule River at Crawford Road, Sequoia National Forest, *Laeger* 345 (CAS).

****Brachythecium oedipodium* (Mitten) A. Jaeger**

[Brachytheciaceae]

Illustrations: Ignatov 1998; Piippo 1983.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Amador Co.: Tiger Reservoir Road above Panther Creek Bridge, *Norris* 103335; Del Norte Co.: Coastal Trail between False Klamath Cove and Requa, Redwood National Park, *Norris* 70363; Fresno Co.: road between Eshom Creek Campground and Redwood Mountain, Whitakers Forest, *Shevock* 18431; Mendocino Co.: Ant Ridge off of Forest Road 25N18, Mendocino National Forest, *Shevock* & *Isle* 15915; Placer Co.: Dutch Flat Reservoir about 2 miles from town of Dutch Flat, *Norris* 101624; Siskiyou Co.: Highway 96 at Ash Creek Bridge, Klamath River, Klamath National Forest, *Norris* 105195.

***Brachythecium plumosum* (Hedwig) Bruch & W. P. Schimper** [Brachytheciaceae]

Literature: Lawton 1971.

Illustrations: Abramov and Volkova 1998; Buck 1998; Ignatov 1998; Ignatov and Koponen 1996;

Ireland 1982; Lawton 1971; Robinson 1962; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Del Norte Co.: Sanger Lake along Forest Road 4803 east of O'Brien, Siskiyou National Forest, *Norris* 70816; El Dorado Co.: near Sayles Canyon Trailhead, Eldorado National Forest, *Norris* 70990; Fresno Co.: east of Idaho Lake, Kaiser Wilderness, Sierra National Forest, *Shevock* 21011; Nevada Co.: Castle Valley north of Boreal Ski Area, Tahoe National Forest, *Norris* 86845; Siskiyou Co.: between Bear Cabin and the Elk Creek Trail along Bear Creek, Marble Mountain Wilderness, Klamath National Forest, *Spjut* 1276 (UC); Trinity Co.: Corral Bottoms Road about 1.5 miles from Big Bar, Shasta-Trinity National Forest, *Norris* 21037; Tulare Co.: Crawford Road, western slope of Slate Mountain, Sequoia National Forest, *Shevock* 18431.

***Brachythecium populeum* (Hedwig) Bruch & W. P. Schimper** [Brachytheciaceae]

Literature: As *Hypnum populeum* Lesquereux 1868; Watson 1880.

Illustrations: Abramov and Volkova 1998; Ignatov 1998; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Fresno Co.: Deer Cove Creek along South Fork Kings River, Sequoia National Forest, *Shevock* 12455; Shasta Co.: Squaw Valley Creek southwest of McCloud, Shasta-Trinity National Forest, *Norris* & *Hillyard* 104290; Siskiyou Co.: junction of South Fork Sacramento River at Soapstone Creek, Shasta-Trinity National Forest, *Norris* 102473; Trinity Co.: Big Creek east of China Peak, *Norris* 76832.

****Brachythecium reflexum* (Starke in Weber & D. Mohr) Bruch & W. P. Schimper**

[Brachytheciaceae]

Illustrations: Ignatov 1998; Lawton 1971; Smith 1978; Williams 1935. As *Brachythecium bestii* Piippo 1983.

Geographic subdivisions: NW, SNE.

Selected specimens: Del Norte Co.: Highway 199 about 8.2 miles east of Highway 101, *Gist* 155 (UC); Inyo Co.: near Dragon Peak above Onion Valley, John Muir Wilderness, Inyo National Forest, *Norris* 46708; Lake Co.: Mt. Sanhedrin above Mill Creek, Mendocino National Forest, *Toren* 7140 (CAS) [determined by McFarland].

***Brachythecium rivulare* Bruch & W. P. Schimper** [Brachytheciaceae]

Literature: Holmberg 1969; Moxley 1928; Spjut 1971.

Illustrations: Abramov and Volkova 1998; Buck 1998; Flowers 1973; Ignatov 1998; Ignatov and Koponen 1996; Ireland 1982; Koponen et al. 1995; Lawton 1971; Robinson 1962; Smith 1978.

Geographic subdivisions: CaR, MP, NW, SN, SNE.

Selected specimens: Humboldt Co.: Forest Road 10N02 at head of Mill Creek, *Norris* 70585; Inyo Co.: Goodale Creek at BLM Goodale Campground, *Shevock & Norris* 16854; Modoc Co.: Cottonwood Flat Campground, Modoc National Forest, *Norris* 68523a; Mono Co.: Lundy Lakes Trail along Mill Creek below Lake Helen, Inyo National Forest, *Norris* 78869; Placer Co.: road to Bowman Lake about 2 miles from Highway 20, Tahoe National Forest, *Norris* 77005; Tulare Co.: Nobe Young Creek, Sequoia National Forest, *Laeger* 12 (CAS) and Oriole Lake, Sequoia National Park, *Norris, Shevock, & Barahona* 87554.

***Brachythecium rutabulum* (Hedwig) Bruch & W. P. Schimper** [Brachytheciaceae]

Literature: Ireland 1982; Kellman 2003; Kingman 1912; McGrew 1976; Shevock and Toren 2001.

Illustrations: Abramov and Volkova 1998; Ignatov 1998; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, CW, MP, NW, SN, SNE.

Selected specimens: Contra Costa Co.: Mitchell Canyon, Mt. Diablo State Park, *Norris* 100609; Fresno Co.: Redwood Creek above Highway 180, Monarch Wilderness, Sequoia National Forest, *Shevock & York* 12681 (determined by Ochyra); Inyo Co.: South Fork Bishop Creek, Inyo National Forest, *Shevock* 12549; Lake Co.: Library Park, Lakeport, *Toren* 7665 (CAS) [determined by McFarland]; Modoc Co.: Deep Creek, 2 miles west of Cederville-Eagleville Road, *Norris* 18728; Santa Cruz Co.: Scotts Valley, *Kellman* 1122 (CAS); Sierra Co.: Highway 49 at Chapman Creek, Tahoe National Forest, *Kellman* 261 (CAS); Tulare Co.: Freeman Grove, Lloyd Meadows Basin, Sequoia National Forest, *Shevock* 3899 and General's Highway near Ash Mountain Headquarters, Sequoia National Park, *Shevock* 16747.

***Brachythecium salebrosum* (Weber & D. Mohr) Bruch & W. P. Schimper** [Brachytheciaceae]

Literature: Holmberg 1969; Ireland 1982; Shevock and Toren 2001; Spjut 1971.

Illustrations: Ignatov 1998; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, DMoj, NW, SN, SNE.

Selected specimens: Fresno Co.: Taboose Pass Trail, headwaters of South Fork Kings River, Kings Canyon National Park, *Shevock* 13855; Inyo Co.: South Fork Hanaupah Canyon, east base of Telescope Peak, Death Valley National Park, *Shevock & York* 21340, 21345 & 21357; Mono Co.: Mormon Meadow in Cinnabar Canyon off of Highway 270, 3 miles east of Highway 395 on road to Bodie, *Shevock* 15337; Shasta Co.: headwaters of Nelson Creek, Lassen National Forest, *Harpel* 16384 (pers. herb.); Siskiyou Co.: Sugar Creek, Klamath National Forest, *McGrew* 87 (UC).

***Brachythecium starkei* (Bridel) Bruch & W. P. Schimper** [Brachytheciaceae]

Literature: Kellman 2003; McGrew 1976; Spjut 1971.

Illustrations: Flowers 1973; Ignatov 1998; Ireland 1982; Lawton 1971; Piippo 1983.

Geographic subdivisions: CW, NW, SN.

Selected specimens: Del Norte Co.: about 0.5 mile north of Lake Earl, *Norris* 70739; Fresno Co.: Mist Falls Trail about 3 miles from Cedar Grove, South Fork Kings River, Kings Canyon National Park, *Shevock & York* 14493 and lower end Fence Meadow, Sierra National Forest, *Laeger* 354 (CAS, UC); Humboldt Co.: College Cove about 0.5 mile from Trinidad, *Norris* 47760; San Bernardino Co.: Highway 18 at Castle Rock Trail, Big Bear Lake, San Bernardino National Forest, *Shevock* 24087; Santa Cruz Co.: City of Santa Cruz, *Kellman* 1830 (CAS).

***Brachythecium velutinum* (Hedwig) Bruch & W. P. Schimper** [Brachytheciaceae]

Literature: Bourell 1981; Harpel 1980a; Harthill et al. 1979; Howe 1897; Ireland 1982; Kellman 2003; Lawton 1965b, 1971; Long 1978; McGrew 1976; Mishler 1978; Showers 1982; Sigal 1975; Spjut 1971; Toren 1977; Yurky 1990, 1995.

Illustrations: Abramov and Volkova 1998; Ignatov 1998; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN, SNE, SW.

Selected specimens: Inyo Co.: South Fork Bishop Creek, 4.2 miles south of Highway 168 along South Fork Road, Inyo National Forest, *Shevock* 12544; Los Angeles Co.: Mt. Baldy area, San Gabriel Mountains, Angeles National Forest, *Harpel* 1328 (pers. herb.); Plumas Co.: Highway 89 about 3 miles south of Crescent Mills, *Norris* 69938; Riverside Co.: Devils Slide Trail, San Jacinto Wilderness, San Bernardino National Forest, *Shevock, Kramer, Hall, & Ward* 24085; Siskiyou Co.: Jackson Creek at Callahan, Klamath National Forest, *Norris* 70497; Trinity Co.: White Rock Road about 3 miles south of Highway 36, *Norris* 56100; Tulare Co.: Highway 190 at Cedar Slope, Sequoia National Forest, *Shevock* 14221.

***Brachythecium venustum* De Notaris** [Brachytheciaceae]

Literature: As *Brachythecium petrophilum* Koch 1950a, 1951e; Koch and Ikenberry 1954. As *Brachythecium velutinum* var. *venustum* Holmberg 1969; Lawton 1965b, 1971.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, SN.

Selected specimens: Del Norte Co.: Bear Creek north of Bear Basin Butte, *Norris* 68887; Fresno Co.: Reese Creek, Forest Road 10S36, Sierra National Forest, *Shevock & Bourell* 13984; Plumas Co.: Chips Creek at Highway 70 west of Belden, *Norris* 70005; Tulare Co.: Bear Creek along road to Mountain Home State Forest, Sequoia National

Forest, *Shevock* 3959 and Oriole Lake, Sequoia National Park, *Norris*, *Shevock*, & *Barahona* 87527.

***Bruchia bolanderi* Lesquereux** [Bruchiaceae]

Literature: Christy and Wagner 1996; Koch 1950a; Lesquereux 1868; Lesquereux and James 1884; Rushing 1986; Showers 1982; Watson 1880. **Illustrations:** Grout 1928–1940; Rushing 1986.

Geographic subdivisions: CaR, SN.

Selected specimens: Nevada Co.: Castle Valley, Tahoe National Forest, *Norris* 86857; Plumas Co.: Quincy-LaPorte Road at Onion Valley, Plumas National Forest, *Norris* 83175; Tehama Co.: near southeast entrance station of Lassen Volcanic National Park, *Showers* 3578 (UC); Tulare Co.: Cold Spring below Portuguese Pass, Greenhorn Mountains, Sequoia National Forest, *Shevock* 14313; Tuolumne Co.: near Piute Meadow, Emigrant Wilderness, Stanislaus National Forest, *Norris* 77107 and between Tuolumne Meadows and Tioga Pass, Yosemite National Park, *Norris* 100360.

***Bruchia flexuosa* (Schwägrichen) C. Müller**

Hal. [Bruchiaceae]

Literature: Kellman 2003; Rushing 1986; Rushing and Christy 1984.

Illustrations: Crum and Anderson 1981; Rushing 1986.

Geographic subdivisions: CW, NW.

Selected specimens: Mendocino Co.: near Willits, *Branscomb* 176 (NY); Santa Cruz Co.: meadow area on north side of Empire Grade, milepost 13, *Kellman* 1456 (CAS) and “four corners” area of UC Santa Cruz Campus, *Kellman* 1459 & 1463 (CAS) [confirmed by Rushing].

***Bryoerythrophyllum columbianum* (F. J.**

Hermann & E. Lawton) Zander [Pottiaceae]

Literature: Zander 1979a. As *Didymodon columbianus* Strid 1974.

Illustrations: Hermann and Lawton 1968; Lewis 1981.

Geographic subdivisions: CaR, NW.

Selected specimens: Colusa Co.: Salt Creek near Fox Canyon, Highway 20 about 8.5 miles east of Lake County line, *Norris* 67518; Lake Co.: Manning Creek, Highway 175 about 4 miles west of Lakeport, *Toren*, *Bourell*, *Dearing*, & *Shevock* 6999 (BUF, CAS) [confirmed by Zander]; Shasta Co.: Liberty Gulch, Whiskeytown National Recreation Area, *Hillyard* 499 (UC).

***Bryoerythrophyllum recurvirostrum* (Hedwig)**

Chen [Pottiaceae]

Literature: Flowers 1973; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; McCleary 1972; Showers 1982; Spjut 1971; Strid 1974; Zander 1978b. As *Didymodon recurvirostris* Koch 1950a; Lawton 1971. As *Didymodon rubellus* Lesquereux 1868; Watson 1880.

Illustrations: Allen 2002; Crum and Anderson

1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: CaR, NW, SN, SNE, SW.

Selected specimens: Mono Co.: Convict Lake Trail about 1.5 miles above Convict Lake, John Muir Wilderness, Inyo National Forest, *Norris* 71344; Riverside Co.: North Fork San Jacinto River, San Jacinto State Park, *Harpel* 1141 (pers. herb.); Siskiyou Co.: Jaynes Creek northwest of Klamath River, *Norris* 48695; Tulare Co.: Rock Creek Canyon, Kern River, Sequoia National Park, *J.T. Howell s.n.* (CAS, NY) and Kern Plateau, slopes of Fish Creek near Rodeo Flat, Sequoia National Forest, *Shevock* 18407 (determined by Zander); Tuolumne Co.: Douglas Flat, Dardanelles, *R.J. Rodin* 6176 (UC).

***Bryolawtonia vancouveriensis* (Kindberg) Norris & Enroth** [Neckeraceae]

Literature: Kellman 2003; Norris and Enroth 1990; Shevock and Toren 2001. As *Bestia holzingeri* Koch 1950a; Koch and Ikenberry 1954. As *Bestia occidentalis* Koch 1950a. As *Bestia vancouveriensis* Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Lawton 1971; McCleary 1972; Yurky 1990. As *Thamnium holzingeri* Howe 1896. As *Poortrichum vancouveriense* Crum 1987; Yurky 1995. **Illustrations:** Lawton 1971. As *Thamnium holzingeri* Renauld and Cardot 1894.

Geographic subdivisions: CW, NW.

Selected specimens: Alameda Co.: Strawberry Canyon about 0.5 mile above UC Botanic Garden, *Norris* 82610; Del Norte Co.: Damnation Creek Trail, Del Norte Redwoods State Park, *Norris* & *Taranto* 10978 & 10980; Humboldt Co.: Cathedral Trees Trail, Prairie Creek Redwoods State Park, *Jamieson* 872 (UC); Lake Co.: Grizzly Canyon between Elk Mountain and Horse Mountain, Mendocino National Forest, *Toren* 7685 (CAS); Marin Co.: trail near Mud Lake, Point Reyes National Seashore, *Norris* 71809; Mendocino Co.: near Ranger Station, Sinkyone Wilderness State Park, *Norris* 71753 and North Coast Range Preserve about 11 km north of Branscomb, *Bourell* 1610 (CAS) [determined by Toren]; San Francisco Co.: Golden Heights Park, *Shevock* 19202 & *Toren* 7943 (CAS); Santa Cruz Co.: Spring Trail, Pogonip Park near UC Santa Cruz, *Kellman* 316 (UC).

***Bryum algovicum* Sendtner ex C. Müller Hal.**

[Bryaceae]

Literature: Crum and Anderson 1981; Spence 1988a. As *Bryum angustirete* Flowers 1973; Harthill et al. 1979; Koch 1950a, 1958; Lawton 1971. As *Bryum pendulum* Koch 1950a.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Smith 1978; Zolotov 2000.

Geographic subdivisions: NW, SN, SNE.

Selected specimens: Kern Co.: Sand Canyon about 3 miles north of Highway 58, southern Piute Mountains, *Hare* 99 (CAS); Mono Co.: near Cottonwood

Creek, White Mountains, Inyo National Forest, *Mitchell* 63 (UC); Siskiyou Co.: South Fork of Salmon River near junction with West Fork, *Norris* 10109.

***Bryum alpinum* Hudson ex Withering**
[Bryaceae]

Literature: Coville 1893; Crum and Anderson 1981; Koch 1950a, 1958; Lawton 1971; McGrew 1976; Spence 1988a.

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Lawton 1971; Sharp et al. 1994; Smith 1978; Zolotov 2000.

Geographic subdivisions: NW, SN.

Selected specimens: Fresno Co.: Baxter Lake, Kings Canyon National Park, *Shevock & York* 16547; Humboldt Co.: Tish-Tang-a-Tang Creek near Grogans Hole, *Norris* 47836 (determined by Spence); Tulare Co.: between Redwood Crossing and Long Meadow, Wishon Fork Tule River, Golden Trout Wilderness, Sequoia National Forest, *Shevock* 10609 (determined by Spence); Tuolumne Co.: Canyon of the South Fork Stanislaus River, *J.T. Howell s.n.* (CAS) [determined by Andrews].

***Bryum amblyodon* C. Müller Hal.** [Bryaceae]

Literature: Spence 1988a. As *Bryum inclinatum* Lesquereux 1868; Watson 1880. As *Bryum stenotrichum* Crum and Anderson 1981; Harthill et al. 1979; Koch 1950a, 1958; Lawton 1971; McGrew 1976; Strid 1974.

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Lawton 1971; Ochrya 1998a; Zolotov 2000.

Geographic subdivisions: NW, SN, SW.

Selected specimens: Fresno Co.: below Kearsarge Pass, Kings Canyon National Park, *Shevock* 14328; Humboldt Co.: Aikens Creek at road to Fish Lake, *Norris* 56387; Riverside Co.: Highway 243 near milepost 25.10, San Jacinto Mountains, San Bernardino National Forest, *Harpel* 1819 (pers. herb.); Sierra Co.: Chapman Creek Campground, Tahoe National Forest, *Tavares* 585 (UC) [determined by Andrews]; Tehama Co.: Beegum Basin north of Yolla Bolly Mountain, Shasta-Trinity National Forest, *Norris* 57034.

***Bryum argenteum* Hedwig** [Bryaceae]

Literature: Bourell 1981; Bradshaw 1926; Brandegee 1891; Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Kellman 2003; Kingman 1912; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Long 1978; Mishler 1978; Shevock and Toren 2001; Showers 1982; Spence 1988a; Steere et al. 1954; Strid 1974; Toren 1977; Watson 1880; Whitemore and Sommers 1999; Yurky 1990, 1995; Zolotov 2000.

Illustrations: Abramov and Volkova 1998; Allen 2002; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton

1971; Ochrya 1998a; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, DMoj, DSon, GV, MP, NW, SN, SNE, SW.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris* 87175; Kern Co.: Highway 178, lower Kern River Canyon about 3 miles east of canyon entrance, Sequoia National Forest, *Shevock* 9131; Riverside Co.: between Key Ranch and Barker Dam, Joshua Tree National Park, *Norris* 50502; San Luis Obispo Co.: about 1 mile west of Poso Summit, *Norris* 55205; Shasta Co.: Highway 299 about 2 miles east of Montgomery Creek, *Norris* 47538.

****Bryum badium* (Bridel) W. P. Schimper**
[Bryaceae]

Illustrations: Nyholm 1987–1998.

Geographic subdivisions: DMoj.

Selected specimens: Inyo Co.: Eagle Spring, Telescope Peak, Death Valley National Park, *York* 2680 (CAS) [determined by Spence].

***Bryum barnesii* Wood in W. P. Schimper**
[Bryaceae]

Literature: Kellman 2003; Vanderpoorten and Zartman 2002.

Illustrations: Vanderpoorten and Zartman 2002; Wilczek and Demaret 1976.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Humboldt Co.: Highway 36 about 2 miles east of Carlotta, *Norris* 48200 (determined by Vanderpoorten); Santa Cruz Co.: Monterey Bay west of Capitola Wharf, *Kellman* 1195 (CAS); Shasta Co.: Highway at Shasta College north of Redding, *Norris* 57779 & 57783 (determined by Vanderpoorten), about 11 miles east of Anderson to Shingleton Road, *Norris* 23731 (determined by Vanderpoorten); Tulare Co.: Clough Cave, Sequoia National Park, *Norris & Shevock* 92744 (determined by Vanderpoorten).

***Bryum bicolor* Dickson** [Bryaceae]

Literature: Bourell 1981; Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Jamieson 1969; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Long 1978; McCleary 1972; Mishler 1978; Shevock and Toren 2001; Steere 1954; Toren 1977; Yurky 1990, 1995. As *Bryum californicum* Brandegee 1891; Lesquereux 1868; Lesquereux and James 1884; Millsbaugh and Nuttall 1923; Sayre 1940; Sullivant 1856.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971; Wilczek and Demaret 1976; Zolotov 2000. As *Bryum dichotomum* Spence 1988a.

Geographic subdivisions: CaR, CW, MP, NW, SN.

Selected specimens: Alpine Co.: Highway 4 about 11 miles west of Woodfords, *Koch* 1804 (UC); Contra Costa Co.: Gibraltar Rock toward summit of Mt. Diablo, *Koch* 1566 (UC); Humboldt Co.: Way County Park, *Norris* 25297 (determined by

Spence); San Francisco Co.: Lafayette Park, San Francisco, *Shevock* 19234; Santa Clara Co.: San Francisquito Creek, Palo Alto, *Drouet* 1333 (UC) [determined by Vanderpoorten]; Shasta Co.: Highway 299 on north side of Haynes Flat about 3 miles west of Burney, *Norris* 68547 (determined by Spence); Tehama Co.: Highway 99 about 3 miles south of Vina, *Norris* 48226 (determined by Vanderpoorten); Tulare Co.: road 1.2 miles above Buckeye Campground, trailhead for Middle Fork Kaweah River Trail, Sequoia National Park, *Shevock* 15207 (determined by Vanderpoorten).

***Bryum bimum* (Schreber) Turner** [Bryaceae]

Literature: Coville 1893; Lesquereux 1868; Spjut 1971.

Illustrations: Abramov and Volkova 1998; Ignatov and Ignatova 2003; Nyholm 1987–1998; Podpěra 1973.

Geographic subdivisions: NW.

Selected specimens: Humboldt Co.: road to Petrolia about 1.5 mile east of ocean shore, *Norris* 76861.

***Bryum blindii* Bruch & W. P. Schimper**
[Bryaceae]

Literature: McGrew 1976; Shaw 1981e; Spence 1988a.

Illustrations: Crum and Anderson 1981; Ireland 1982; Lawton 1971.

Geographic subdivisions: GV.

Selected specimens: Butte Co.: Thermalito near Oroville Airport, Thermalito Afterbay, *Ahart* 10024, 10025 (UC); Solano Co.: Jepson Prairie Ecological Reserve, *Norris* 101397.

***Bryum caespiticium* Hedwig** [Bryaceae]

Literature: Bourell 1981; Cooke 1941; Coville 1893; Crum and Anderson 1981; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Long 1978; McGrew 1976; Mishler 1978; Spence 1988a; Spjut 1971; Strid 1974; Toren 1977.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, MP, NW, SN, SNE.

Selected specimens: Inyo Co.: South Lake Road, 0.7 mile below South Lake, Inyo National Forest, *Shevock* 12539; Lake Co.: Hull Mountain, Mendocino National Forest, *Toren* 857 (UC); Monterey Co.: cemetery on Lockwood Road about 2 km east of Alamo Air Strip, Hunter-Liggett Military Reservation, *Norris* 87337; Placer Co.: near entrance to Squaw Valley, *Tavares & Noack* 628 (UC) [determined by Andrews]; Siskiyou Co.: near South Sanger Lake, *Norris & McGrew* 45628 and trail to Long Gulch southwest of Callahan, Klamath National Forest, *Norris* 74868.

***Bryum calobryoides* Spence** [Bryaceae]

Literature: Kellman 2003; Spence 1986, 1988a.

Illustrations: Spence 1986.

Geographic subdivisions: CaR, CW, NW, SN, SNE, SW.

Selected specimens: Butte Co.: Upper Bidwell Park between Big Chico Creek and Sycamore Creek, *Janeway* 6979 (UC); Kern Co.: Pine Tree Canyon, *Shevock, Ertter, & Hare* 17831 (determined by Spence); Mono Co.: Koenig Lake east of Sonora Pass, Toiyabe National Forest, *Norris* 57164; Santa Cruz Co.: Laurel Road at Highway 17, *Kellman* 2673 (CAS) [confirmed by Spence]; Siskiyou Co.: Terrace and Upper Cliff Lakes, *Norris* 52999; Tehama Co.: west face of North Yolla Bolly Mountain, Shasta-Trinity National Forest, *Norris* 57072; Trinity Co.: Packer's Peak, *Norris* 8973 (determined by Spence).

***Bryum canariense* Bridel** [Bryaceae]

Literature: Harthill et al. 1979; Holmberg 1969; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; McCleary 1972; McGrew 1976; Shevock and Toren 2001; Showers 1982; Spence 1988a; Spjut 1971; Steere 1954; Toren 1977; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Bryum hendersonii* Howe 1896; Renauld and Thériot 1890. As *Bryum provinciale* Lesquereux and James 1884; Watson 1880. **Illustrations:** Allen 2002; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: CW, DMoj, DSon, NW, SN, SNE.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris* 87206; Humboldt Co.: South Fork Tish-Tang-a-Tang Creek east of Hoopa, *Norris & Whittemore* 52404; Mono Co.: Mormon Meadow and Clearwater Creek, Highway 270 about 3 miles east of Highway 395 on road to Bodie, *Shevock* 15248; San Bernardino Co.: Coyote Canyon, Granite Mountains north of Highway 40 and east of Needles, Mojave National Preserve, *Norris* 87852; San Francisco Co.: Fort Winfield Scott, Presidio of San Francisco, *Shevock* 19369; Tulare Co.: end of County Road 348 near Clough Cave, South Fork Kaweah River, Sequoia National Park, *Shevock* 12998.

***Bryum capillare* Hedwig** [Bryaceae]

Literature: Bourell 1981; Bradshaw 1926; Crum and Anderson 1981; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Long 1978; McCleary 1972; McGrew 1976; Mishler 1978; Shevock and Toren 2001; Showers 1982; Sigal 1975; Smith 1970; Spence 1988a; Spjut 1971; Steere 1954; Steere et al. 1954; Strid 1974; Toren 1977; Watson 1880; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Bryum sanguilentum* Cardot and Thériot 1904; Howe 1896. As *Bryum subdrepanocladum* Cardot and Thériot

1904. As *Bryum obconicum* Kingman 1912; Lesquereux 1868; Lesquereux and James 1884; Mills-paugh and Nuttall 1923; Sayre 1940; Sullivant 1856. As *Bryum occidentale* Brandegees 1891; Lesquereux 1868; Lesquereux and James 1884; Sullivant 1856. As *Rosulabryum capillare* Kellman 2003.

Illustrations: Abramov and Volkova 1998; Allen 2002; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978; Syed 1973; Zolotov 2000.

Geographic subdivisions: CaR, CW, NW, SN, SNE.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris 87214*; El Dorado Co.: Traverse Creek Botanical Area about 2.5 air miles southeast of Georgetown, Eldorado National Forest, *Shevock 12247*; Monterey Co.: bluffs at the Pinnacles, Hunter Liggett Military Reservation, *Norris 87292*; Sonoma Co.: The Cedars north of Cazadero, *Ertter & Raiche 12864* (UC); Tulare Co.: General's Highway 0.6 mile west of Clover Creek, Sequoia National Park, *Shevock & Tseng 15757*.

***Bryum cyclophyllum* (Schwägrichen) Bruch & W. P. Schimper** [Bryaceae]

Literature: Spence 1988a. As *Bryum tortifolium* Koch 1951b; McGrew 1976.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Zolotov 2000.

Geographic subdivisions: NW.

Selected specimens: Lake Co.: along Bartlett Springs Road, *J.W. Carmiggelt 50* (UC) and Oakwood Springs, BLM Cow Mountain Recreation Area, *Toren 6889* (CAS) [determined by Spence]; Tehama Co.: west face of North Yolla Bolly Mountain, Shasta-Trinity National Forest, *Norris 57062* & 57070.

****Bryum elegans* Nees in Bridel** [Bryaceae]

Illustrations: Ignatov and Ignatova 2003; Smith 1978.

Geographic subdivisions: NW, SN.

Selected specimens: Lake Co.: canyon below Forest Road M-3 at Low Gap, Mendocino National Forest, *Toren, Dearing, & Shevock 7724* (CAS) [determined by Spence]; Nevada Co.: Forest Road 18 at Fall Creek between Bowman Lake and Highway 20, *Shevock, Ertter, & Morosco 15703* (determined by Muñoz; confirmed by Spence).

***Bryum erythroloma* (Kindberg) Syed** [Bryaceae]

Literature: Spence 1988a.

Illustrations: Allen 2002; Sharp et al. 1994; Syed 1973.

Geographic subdivisions: NW.

Selected specimens: Humboldt Co.: Redwood Valley Road about 0.65 mile from Highway 299, *Farr 93* (UC) and Johnson Prairie, *Norris 19039*; Lake

Co.: Tule Lake, Mt. Sanhedrin, Mendocino National Forest, *Toren & Dearing 7192* (CAS) [determined by Spence] and Mt. Konocti at Buckingham Bluffs above Clear Lake, *Shevock, Heise, Toren, & Harpel 20605*.

***Bryum flaccidum* Bridel** [Bryaceae]

Literature: Spence 1988a; Whittemore and Sommers 1999.

Illustrations: Syed 1973.

Geographic subdivisions: CaR, NW, MP, SN.

Selected specimens: El Dorado Co.: near Round Lake, Eldorado National Forest, *Norris 71160* (determined by Spence); Lake Co.: Hidden Valley north of Middletown, *Toren & Dearing 7577* (CAS) [determined by Spence]; Modoc Co.: west side of Goose Lake about 4 miles south of Oregon state line, *Norris 18722*; Siskiyou Co.: Soda Creek Road about 4 miles northeast of Highway 5 near Dunsmuir, Shasta-Trinity National Forest, *Norris 84809*; Trinity Co.: Big Canyon at Hayfork Creek, *Norris 56151*; Tulare Co.: below Paradise Ridge overlooking Middle Fork Kaweah River, Sequoia National Park, *Shevock 14632*.

***Bryum gemmascens* Kindberg** [Bryaceae]

Literature: Shevock and Toren 2001; Spence 1988a.

Illustrations: Syed 1973; Wilczek and Demaret 1976.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Fresno Co.: north-facing slope of Red Mountain southwest of Tollhouse, *York 1613* (CAS); Humboldt Co.: East Fork about 5 air miles north of Mad River, Six Rivers National Forest, *Norris 83904*; Lake Co.: Highway 53 about 1 mile south of Highway 20, *Norris 47656* (determined by Spence); San Francisco Co.: Bernal Heights Park, *Toren 7792* (CAS); Tehama Co.: Battle Creek along Highway 36 at milepost 75, *Norris 52571* (determined by Spence); Trinity Co.: Stuart Gap Trailhead, *Norris 56853* (determined by Spence).

***Bryum gemmiferum* R. Wilczek & Demaret** [Bryaceae]

Literature: Blockeel et al. 2001; Kellman 2003; Vanderpoorten and Zartman 2002.

Illustrations: Smith 1978; Vanderpoorten and Zartman 2002; Wilczek and Demaret 1976.

Geographic subdivisions: CW.

Selected specimens: San Mateo Co.: Montara State Beach, *Vanderpoorten 4782* (DUKE); Santa Cruz Co.: Scotts Valley Drive, Scotts Valley, *Kellman 1178* (CAS).

***Bryum gemmilucens* R. Wilczek & Demaret** [Bryaceae]

Literature: Kellman 2003; Shevock and Toren 2001; Spence 1988a.

Illustrations: Smith 1978.

Geographic subdivisions: CaR, CW, NW.

Selected specimens: Butte Co.: levee of Feather River north of Gridley, *Norris* 52542 (determined by Vanderpoorten); Marin Co.: South Novato, *Jenkinson s.n.* (UC) [determined by Vanderpoorten]; Napa Co.: Crane Park, City of St. Helena, *Norris* 48240 (determined by Spence; Vanderpoorten); Lake Co.: Chalk Mountain, North Fork Cache Creek, *Toren & Dearing* 7323 (CAS) and town of Nice, east shore of Clear Lake, *Toren* 7710 (CAS) [determined by Spence]; San Francisco Co.: Aqua Vista Park, Central Basin, San Francisco, *Shevock* 18993; Shasta Co.: Sacramento River Trail northeast of Redding, *Norris* 105297; Siskiyou Co.: Klamath River at Ash Creek Bridge, Klamath National Forest, *Norris & Hillyard* 105241; Sonoma Co.: at summit ridge behind Armstrong Park, *Koch* 3532 (UC) [determined by Vanderpoorten].

***Bryum gemmiparum* De Notaris** [Bryaceae]

Literature: Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Long 1978; Mishler 1978; Spence 1988a; Spjut 1971; Strid 1974; Toren 1977.

Illustrations: Crum and Anderson 1981; Flowers 1973; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, CW, DMoj, DSon, MP, NW, SN, SW.

Selected specimens: Del Norte Co.: Smith River about 10 miles east of Gasquet on Highway 199, *Norris* 8787; Lake Co.: Soda Creek near Lake Pillsbury, Mendocino National Forest, *Toren* 5131 (CAS); Modoc Co.: west side Goose Lake about 4 miles south of Oregon state line, *Norris* 18720; Plumas Co.: Highway 70 near Belden, *Norris* 69975; Riverside Co.: Lilly Creek, County Park near Idyllwild, San Jacinto Mountains, *Harpel* 1450 (pers. herb.); San Bernardino Co.: Cottonwood Wash, Granite Mountains, Mojave National Preserve, *Laeger & Bucknar* 1837 (CAS) [determined by Spence]; Shasta Co.: Highway 299 at Casberry Flat about 1 mile west of Hatchet Mountain Summit, *Norris* 68581 (determined by Spence).

***Bryum laevifilum* Syed** [Bryaceae]

Literature: Kellman 2003.

Illustrations: Ignatov and Ignatova 2003; Syed 1973.

Geographic subdivisions: CW, SNE.

Selected specimens: Mono Co.: Secret Lake, Toiyabe National Forest, *Norris* 77054; Santa Cruz Co.: Highway 17 at Laurel Road, *Kellman* 2702 (CAS) [confirmed by Spence].

***Bryum lanatum* (Palisot de Beauvois) Bridel** [Bryaceae]

Literature: Spence 1988a. As *Bryum argenteum* var. *lanatum* Crum and Anderson 1981; McCleary 1972; Millsbaugh and Nuttall 1923; Sayre 1940; Steere 1954; Steere et al. 1954.

Illustrations: Crum and Anderson 1981; Smith 1978.

Geographic subdivisions: SN.

Selected specimens: Fresno Co.: South Fork Kings River near Boyden Cave, Monarch Wilderness, Sequoia National Forest, *York* 503 (CAS) and Haslett Basin, Sierra National Forest, *Norris, Shevock, & Barahona* 87448; Tulare Co.: Wishon Fork Tule River above Doyle Springs and Camp Wishon, Sequoia National Forest, *Norris, Shevock, & Barahona* 87030.

***Bryum lisae* De Notaris** [Bryaceae]

Literature: Kellman 2003; Shevock and Toren 2001; Spence 1988a. As *Bryum cirrhatum* Lesquereux 1868; Lesquereux and James 1884; Watson 1880. As *Bryum creberrimum* Bourell 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Lawton 1971; McCleary 1972; McGrew 1976; Strid 1974; Toren 1977. As *Bryum cuspidatum* Cooke 1941; Steere 1954. As *Bryum intermedium* Lesquereux 1868; Millsbaugh and Nuttall 1923; Sulivant 1856. As *Bryum lisae* var. *cuspidatum* Yurky 1990, 1995. As *Bryum lonchocaulon* Flowers 1973; Harpel 1980a; Harthill et al. 1979; Koch 1950a, 1951e; Koch and Ikenberry 1954; Strid 1974.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ireland 1982; Lawton 1971; Smith 1973.

Geographic subdivisions: CaR, CW, NW, SN, SNE, SW.

Selected specimens: Kern Co.: north of Tiger Flat Campground, Greenhorn Mountains, Sequoia National Forest, *Shevock* 10628; Inyo Co.: South Lake Road 0.7 mile below South Lake, Inyo National Forest, *Shevock* 12536; Riverside Co.: Bighorn Overlook along Highway 74 at eastern boundary of San Bernardino National Forest, *Norris* 57833; San Francisco Co.: Presidio of San Francisco, *Shevock* 19353; Tehama Co.: Fork of Beegum Creek about 1.5 miles west of Rat Trap Gap, *Norris* 56994 (determined by Spence).

***Bryum meesioides* Kindberg in Macoun** [Bryaceae]

Literature: Ireland 1977; Spence 1988a.

Illustrations: Ireland 1977.

Geographic subdivisions: NW.

Selected specimens: According to Spence (personal communication) a California packet was determined to be this species. We have reviewed the *Bryum* holdings at CAS, MO, NY, UBC and UC and have not been able to locate a collection of *Bryum meesioides* from California. According to Ireland (1977), the gametophyte of this species is nearly indistinguishable from that of *Bryum pallens* but several diagnostic characters of the sporophyte readily separate these two related taxa. It is probable that *Bryum meesioides* remains among undetermined *Bryum* collections in California herbaria. We expect it to be documented for northern California.

****Bryum microerythrocarpum* C. Müller Hal. & Kindberg** [Bryaceae]

Illustrations: Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, CW, NW.

Selected specimens: Humboldt Co.: near Dickson Butte, *Kirn & Nomura 117b* (UC) and Long Ridge about 26 miles north of Big Hill Road, *Norris 47788* (determined by Spence); Mendocino Co.: Pygmy Cypress Forest about 5 miles east of Albion, *Norris 11785 & 11786*; Santa Cruz Co.: railroad tracks near Rincon Road, Henry Cowell Redwoods State Park, *Kellman 616* (UC); Tehama Co.: Highway 36 at Georgie Dells Road, *Norris 56060*.

***Bryum miniatum* Lesquereux** [Bryaceae]

Literature: Bourell 1981; Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Howe 1896; Jamieson 1969; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Long 1978; McGrew 1976; Mishler 1978; Showers 1982; Spence 1988a; Spjut 1971; Toren 1977; Watson 1880; Yurky 1990, 1995. As *Bryum atwateriae* Lesquereux and James 1884; Phelps 1878; Watson 1880.

Illustrations: Crum and Anderson 1981; Flowers 1973; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: CaR, CW, NW, SN, SNE, SW.

Selected specimens: Alpine Co.: Red Lake Creek, Tiyoabe National Forest, *Norris 88124*; Del Norte Co.: Smith River along Highway 199 about 9 miles east of junction with Highway 101, Six Rivers National Forest, *Norris 85001*; Mariposa Co.: base of Yosemite Falls, Yosemite National Park, *Koch 1686* (UC); Napa Co.: Napa-Monticello Road, *Koch 1367* (UC); Riverside Co.: Fleming Ranch Road, San Jacinto Mountains, San Bernardino National Forest, *Harpel 2970* (pers. herb.); Santa Cruz Co.: Big Basin State Park, *Kellman 694* (CAS) [determined by Spence]; Tulare Co.: between Redwood Crossing and Long Meadow, Wishon Fork Tule River, Golden Trout Wilderness, Sequoia National Forest, *Shevock 10609*.

***Bryum muehlenbeckii* Bruch & W. P. Schimper** [Bryaceae]

Literature: Crum and Anderson 1981; Holmberg 1969; Koch 1950a; McGrew 1976; Showers 1982; Spence 1988a; Toren 1977.

Illustrations: Crum and Anderson 1981; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Mariposa Co.: Highway 49 about 3.3 miles southeast of Mariposa at junction with Highway 140, *Shevock 15242*; Shasta Co.: Highway at Shasta College north of Redding, *Norris 57789*; Tulare Co.: below Paradise Ridge overlooking the Middle Fork Kaweah River, Sequoia National Park, *Shevock 14633*.

***Bryum pallens* Swartz** [Bryaceae]

Literature: Holmberg 1969; Koch 1958; McGrew 1976; Showers 1982; Spence 1988a; Spjut 1971; Toren 1977.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1977; Lawton 1971; Zolotov 2000.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Butte Co.: opposite spillway of Oroville Dam, *Norris 52557*; Kern Co.: Pine Tree Canyon about 4 miles west of Highway 14, southern Piute Mountains, *Hare 110* (CAS); Contra Costa Co.: Mitchell Canyon, Mt. Diablo State Park, *Norris 100611*; Lake Co.: head of Mill Creek, Mt. Sanhedrin, Mendocino National Forest, *Toren, Heise, & Dearing 7633* (CAS); Mendocino Co.: Covelo Road about 3.1 miles east of Longvale, *Norris 21727*; Plumas Co.: Feather River Canyon about 1 mile inside Plumas National Forest boundary, *Norris 52620*; Trinity Co.: Underwood Mountain Road near junction road to Big Lake, *Norris 10915*.

***Bryum pallescens* Schleicher ex Schwägrichen** [Bryaceae]

Literature: Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; McGrew 1976; Showers 1982; Sigal 1975; Spence 1988a; Spjut 1971; Strid 1974. As *Bryum subrotundum* Lesquereux 1868; Lesquereux and James 1884; Watson 1880.

Illustrations: Allen 2002; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Ochrya 1998a; Sharp et al. 1994; Smith 1973, 1978; Zolotov 2000.

Geographic subdivisions: CaR, MP, NW, SN, SNE, SW.

Selected specimens: Humboldt Co.: Beach Lagoon, *Jamieson 857* (UC); Inyo Co.: Taboose Pass Trail, John Muir Wilderness, Inyo National Forest, *Shevock 16616* (determined by Spence); Mendocino Co.: Little Red Mountain, *Sigal s.n.* (UC); Modoc Co.: near Post Canyon north of Adin, *Norris 47412*; San Bernardino Co.: South Fork Meadows, San Geronio Wilderness, San Bernardino National Forest, *Harpel 2186* (pers. herb.); Shasta Co.: road to Castle Lake at Castle Lake Creek, Shasta-Trinity National Forest, *Norris & Hillyard 103841*; Siskiyou Co.: Jaynes Creek northwest of Klamath River, *Norris 48693*; Tulare Co.: streamlet above Dorst Creek Campground, Sequoia National Park, *Shevock & Dennis 14100*.

***Bryum pseudotriquetrum* (Hedwig) Gärtner, B. Meyer & Scherbius** [Bryaceae]

Literature: Bourell 1981; Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Long 1978; McGrew 1976; Shevock and Toren 2001; Showers 1982; Spence 1988a; Steere et al. 1954; Strid 1974; Toren 1977; Watson 1880; Yurky 1990, 1995. As *Bryum crassirameum* Holmberg 1969; Howe 1896; Koch 1950a; Koch and Ikenberry 1954; Spjut 1971. As *Bryum firmum* Cooke

1941. As *Bryum flagellosum* Koch 1950a, 1958; Koch and Ikenberry 1954. As *Bryum pseudotriquetrum* var. *crassirameum* Toren 1977; Yurky 1990.

Illustrations: Abramov and Volkova 1998; Allen 2002; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Ochrya 1998a; Sharp et al. 1994; Smith 1978; Zolotov 2000.

Geographic subdivisions: CaR, CW, MP, NW, SN, SNE, SW.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris* 87161; Riverside Co.: Vista Grand Guard Station, San Jacinto Mountains, San Bernardino National Forest, *Harpel* 977 (pers. herb.); Shasta Co.: Highway 89 about 21 miles east of McCloud, *Norris & Hermann* 22646; Tulare Co.: Big Meadows off of Forest Road 14S11, Sequoia National Forest, *Shevock & York* 13673; Tuolumne Co.: Pilot Ridge, Stanislaus National Forest, *Shevock* 13274.

***Bryum pyriferum* Crundwell & H. Whitehouse** [Bryaceae]

Literature: Kellman 2003; Shevock and Toren 2001.

Illustrations: Crundwell and Whitehouse 1981.

Geographic subdivisions: CaR, CW, DMoj.

Selected specimens: Lake Co.: west of Butte Rock near Yolo County line, *Toren & Dearing* 8616 (CAS) [confirmed by Spence]; San Bernardino Co.: Clark Mountain, Mojave National Preserve, *Laeger* 1308 (CAS) [determined by Spence]; San Francisco Co.: Alcatraz Island, Golden Gate National Recreation Area, *Toren, Shevock, & Thomas* 8459 (CAS) [confirmed by Spence]; Santa Cruz Co.: Enchanted Loop Trail along Baldwin Creek, Wilder Ranch State Park, *Kellman* 2583 (CAS) and Aptos Creek, *Kellman* 2041 (CAS) [determined by Spence].

***Bryum radiculosum* Bridel** [Bryaceae]

Literature: Spence 1988a.

Illustrations: Crum and Anderson 1981; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CW, NW.

Selected specimens: Del Norte Co.: Gasquet Toll Road at Eighteen Mile Creek, *Norris* 55685 (determined by Spence); San Mateo Co.: Spring Canyon Road, Filioi Center just north of Woodside, *Whittemore* 4415 (CAS).

***Bryum rubens* Mitten** [Bryaceae]

Literature: Crum and Anderson 1981; Crundwell and Whitehouse 1978; Spence 1988a; Yurky 1990, 1995.

Illustrations: Ignatov and Ignatova 2003; Smith 1978; Zolotov 2000.

Geographic subdivisions: CW, NW.

Selected specimens: Lake Co.: off of Morgan Valley Road, BLM Knoxville Recreation Area, *Toren & Dearing* 7066 (CAS) [determined by Spence]. Marin Co.: San Pedro Road at milepost 4.91, *Yurky* 388 (SFSU).

***Bryum subapiculatum* Hampe** [Bryaceae]

Literature: Kellman 2003; Spence 1988a.

Illustrations: Ignatov and Ignatova 2003; Sharp et al. 1994; Zolotov 2000.

Geographic subdivisions: CW.

Selected specimens: Santa Cruz Co.: near Rincon, Henry Cowell Redwoods State Park, *Kellman* 616 (CAS) [determined by Spence] and near Felton, *Kellman* 1318 (CAS), and Yellow Bank Creek, *Kellman* 2090 (CAS).

***Bryum tenuisetum* Limpricht** [Bryaceae]

Literature: Crum and Anderson 1981; Lawton 1971; Spence 1988a; Toren 1977.

Illustrations: Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: GV, SN.

Selected specimens: Fresno Co.: Roaring River Falls above South Fork Kings River, Kings Canyon National Park, *Shevock* 13760; Solano Co.: Campus of the University of California, Davis, *Norris* 48232.

***Bryum torquescens* Bruch** [Bryaceae]

Literature: Howe 1896; Kingman 1912; Lesquereux 1868; Lesquereux and James 1884; Millspaugh and Nuttall 1923; Sayre 1940; Shevock and Toren 2001; Spence 1988a; Sullivant 1856; Watson 1880.

Illustrations: Smith 1978; Syed 1973.

Geographic subdivisions: CW, NW, SN.

Selected specimens: Kern Co.: Highway 178 about 2 miles west of Live Oak Campground east of Bakersfield, *Norris* 70110 (determined by Spence); Fresno Co.: below West Meadow near Sand Flat, Sierra National Forest, *Shevock* 14195; Lake Co.: Robinson Creek east of Highway 29 along Bridge Arbor Road, *Toren & Dearing* 8667 (CAS) [confirmed by Spence]; San Francisco Co.: Lone Mountain Campus, University of San Francisco, *Shevock* 19334.

***Bryum turbinatum* (Hedwig) Turner** [Bryaceae]

Literature: Flowers 1973; Harpel 1980a; Harthill et al. 1979; Kingman 1912; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; McGrew 1976; Spence 1988a; Strid 1974; Yurky 1990, 1995.

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Lawton 1971; Smith 1978; Zolotov 2000.

Geographic subdivisions: CaR, CW, NW, MP, SN, SNE, SW.

Selected specimens: Del Norte Co.: Whiskey Lake, Six Rivers National Forest, *Norris* 57707a; Lassen Co.: Termo-Grasshopper Road about 12 miles west of Termo, *Norris & Hermann* 22639; Mono Co.: Barney Lake, Toiyabe National Forest, *Norris* 67107; Riverside Co.: Round Valley, San Jacinto State Park, *Harpel* 1068 (pers. herb.); Siskiyou Co.: headwaters of Preston Peak, Klamath National Forest, *Norris* 23242; Tulare Co.: Lloyd

Meadows Basin, Sequoia National Forest, *Shevock 4433* and Mosquito Lake Trail, Mineral King, Sequoia National Park, *Shevock & O'Brien 15934* (determined by Spence).

***Bryum uliginosum* (Bridel) Bruch & W. P. Schimper** [Bryaceae]

Literature: Flowers 1973; Koch 1950a; Watson 1880. As *Bryum cernuum* Lesquereux 1868; Watson 1880.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Smith 1978; Zolotov 2000.

Geographic subdivisions: SN.

Selected specimens: Tulare Co.: between Redwood Crossing and Long Meadow, Wishon Fork Tule River, Golden Trout Wilderness, Sequoia National Forest, *Shevock 10604* and headwaters of Freeman Creek, 0.5 mile east of Quaking Aspen, Sequoia National Forest, *Shevock 10638*.

***Bryum violaceum* Crundwell & Nyholm** [Bryaceae]

Literature: Crum and Anderson 1981; Kellman 2003; Lawton 1971; Spence 1988a; Toren 1977; Yurky 1990, 1995.

Illustrations: Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Smith 1978; Zolotov 2000.

Geographic subdivisions: CaR, CW, DMoj, DSon, NW, SN, SW.

Selected specimens: Contra Costa Co.: Mt. Diablo State Park, *Norris 100525*; Fresno Co.: Middle Fork Kings River near LeConte Ranger Station, Kings Canyon National Park, *Shevock & Haultain 18628* (determined by Allen); Lake Co.: end of Hells Peak Road, *Toren 843* (CAS); Marin Co.: Pike County Gulch, *Yurky 309* (SFSU); Monterey Co.: Sam Jones Road about 1 km east of Piojo Airstrip, Hunter-Liggett Military Reservation, *Norris 87220 & 87221*; San Bernardino Co.: Pachalka Spring, Clark Mountain, Mojave National Preserve, *Laeger, Newman & Adams 1800* (CAS) [determined by Spence]; Santa Cruz Co.: Bonny Doon, *Kellman 917* (CAS).

***Bryum weigelii* Sprengel** [Bryaceae]

Literature: Bourell 1981; Crum and Anderson 1981; Flowers 1973; Koch 1950a, 1958; Koch and Ikenberry 1954; Lawton 1971; McGrew 1976; Showers 1982; Spence 1988a; Spjut 1971. As *Bryum duvallii* Lesquereux 1868; Lesquereux and James 1884; Watson 1880.

Illustrations: Abramov and Volkova 1998; Allen 2002; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Zolotov 2000.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Humboldt Co.: Jacoby Creek Road near Quarry southeast of Arcata, *Norris 68250* (determined by Spence); Mariposa Co.: Half Moon Meadow, Yosemite National Park, *Shevock, Wilken, & Fritzke 18501* (determined by Spence);

Siskiyou Co.: Scott Camp Creek Basin, *Norris 53094*; Tulare Co.: Big Meadow off of Forest Road 14S11, Sequoia National Forest, *Shevock & York 13663*.

***Buckiella undulata* (Hedwig) Ireland** [Hypnaceae]

Literature: As *Hypnum undulatum* Lesquereux 1868; Watson 1880. As *Plagiothecium undulatum* Holmberg 1969; Howe 1897; Ireland 1985, 1986; Jamieson 1969; Koch 1950a; Lawton 1971; Smith 1970. See also Ireland 2001.

Illustrations: Ireland 1985; Lawton 1971.

Geographic subdivisions: CW, NW.

Selected specimens: Del Norte Co.: trail between Requa and False Klamath Cove, Redwood National Park, *Norris 24064*; Humboldt Co.: north of Elk Grove Park Headquarters, Prairie Creek Redwoods State Park, *Shevock 16738* and Highway 101 at Seawood Drive about 2 miles north of Trinidad, *Shevock 16730*; Marin Co.: Old Pine Trail, Point Reyes National Seashore, *Robertson 1872* (UC) & 1886 (CAS); Mendocino Co.: County Road 409 about 1 mile east of Highway 1 south of Fort Bragg, *Norris 11688* and Near Little River, *Boyd & Kelly s.n.* (CAS).

***Buxbaumia aphylla* Hedwig** [Buxbaumiaceae]

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971.

Geographic subdivisions: NW.

Selected specimens: Humboldt Co.: shores of Lake Prairie, *Norris 50408*; east of Korbel Road about 12 miles from Blue Lake, *D.E. Jackson 876* (UC).

***Buxbaumia piperi* Best** [Buxbaumiaceae]

Literature: Christy and Wagner 1996; Holmberg 1969; Jamieson 1969; Jamieson and Holmberg 1969; Lawton 1971; Toren and Sigal 1974.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, NW.

Selected specimens: Del Norte Co.: Gasquet-Orleans Road, 0.5 mile from Big Flat Road, Six Rivers National Forest, *Norris & Piippo 82421*; Humboldt Co.: Bill Hill Road at South Fork Mill Creek, *Norris 58647*, Forest Road 10N02, head of Mill Creek, Six Rivers National Forest, *Norris 70567* and Redwood Valley Road about 1 mile north of Highway 299, *Norris 48281*; Mendocino Co.: Jackson State Forest near Mendocino, *Oberlander s.n.* (SFSU), Mendocino Woodlands Camp about 20 km east of Mendocino, *Toren 613* (SFSU) and *Toren & Bourell 1478* (SFSU); Siskiyou Co.: Shadow Creek about 6 miles northeast of Cecilville, *Norris 70553* and Haypress Meadows, Marble Mountain Wilderness, Klamath National Forest, *Norris 12419*.

***Buxbaumia viridis* (A. P. de Candolle) Mougeot & Nestler** [Buxbaumiaceae]

Literature: As *Buxbaumia indusiata* Spjut 1971.

Illustrations: Lawton 1971.

Geographic subdivisions: NW.

Selected specimens: Humboldt Co.: near Pilot Rock, Six Rivers National Forest, *McFarland 01JRM61202* (UC) [determined by Harpel]; Mendocino Co.: Demonstration Forest, Highway 128 near Navarro, *Parsons 113* (SFSU), *Desjardin 2581* (SFSU) and *Giles 121* (SFSU); Trinity Co.: Forest Road 33N45 about 2 miles east of Big Creek Campground, Klamath National Forest, *Jennings 99-012* (UC) [determined by Harpel].

***Calliergonella cuspidata* (Hedwig) Loeske**
[Hypnaceae]

Literature: Ireland 1982; Kellman 2003; Lawton 1971; Shevock and Toren 2001.

Illustrations: Buck 1998; Hedenäs 1993a, 2003; Ireland 1982; Kanda 1978; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: CW, NW.

Selected specimens: Alameda Co.: Mountain View Cemetery, *J.T. Howell s.n.* (UC); Humboldt Co.: bog at Big Lagoon County Park, *Norris 46062 & 46063*; San Francisco Co.: campus lawns at San Francisco State University, *Showers 450* (UC) and *Desjardin 2691* (SFSU), McLaren Park, *Shevock 19136* and Fort Mason, Golden Gate National Recreation Area, *J.T. Howell s.n.* (CAS); Santa Cruz Co.: City of Santa Cruz, *Kellman 1826* (CAS).

****Campylium chrysophyllum* (Bridel) J. M. Lange** [Campyliaceae]

Illustrations: Buck 1998; Flowers 1973; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978. As *Campyliadelphus chrysophyllum* Hedenäs 2003.

Geographic subdivisions: SN, SNE.

Selected specimens: Inyo Co.: Lone Pine Creek at Alabama Hills, *Shevock & Norris 16856*; Mono Co.: above Mildred Lake, John Muir Wilderness, Inyo National Forest, *Norris 71395*; Tulare Co.: Crescent Meadow at Giant Forest, Sequoia National Park, *Shevock 16670* and Holby Meadow near the Ponderosa, Sequoia National Forest, *Shevock 16532*.

***Campylium hispidulum* (Bridel) Mitten**
[Campyliaceae]

Literature: Spjut 1971.

Illustrations: Flowers 1973; Ireland 1982; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: NW, SN.

Selected specimens: Siskiyou Co.: west end English Lake, Marble Mountain Wilderness, Klamath National Forest, *Spjut 1598* (UC); Jaynes Creek at headwaters, northwest of Klamath River, Klamath National Forest, *Norris 48680* (determined by Giles); Tulare Co.: Twisselmann Botanical Area near Sirretta Pass, Kern Plateau, Sequoia National Forest, *Shevock 18418*.

***Campylium polygamum* (W. P. Schimper) C. E. O. Jensen** [Campyliaceae]

Literature: As *Campylium polygamum* var. *fluitans* Koch 1950a. As *Drepanocladus polygamus* Hedenäs 1997a.

Illustrations: Flowers 1973; Ireland 1982; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Fresno Co.: Rowell Meadow, Jennie Lakes Wilderness, Sequoia National Forest, *Shevock & York 13706 & 13715* (determined by Ochrya); Inyo Co.: Warm Springs, White Mountains, *Laeger 1455* (CAS) [determined by Hedenäs]; Lake Co.: Tule Lake, Mt. Sanhedrin, *Toren 5101* (CAS) and *Shevock, Erter, Toren, & Dearing 19487*; Mendocino Co.: pond off of Ant Ridge, Mendocino National Forest, *Shevock & Isle 15912*; Plumas Co.: Gray Eagle Valley floating in ponds, *Leiberg 5495* (EGB); Siskiyou Co.: trail to English Lake between wilderness boundary and Abbott Ranch, Klamath National Forest, *Spjut 1379* (UC); Tulare Co.: Crescent Meadow, Giant Forest, Sequoia National Park, *Shevock 16672* (determined by Ochrya).

***Campylium stellatum* (Hedwig) C. E. O. Jensen**
[Campyliaceae]

Literature: Koch 1958.

Illustrations: Buck 1998; Flowers 1973; Hedenäs 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Fresno Co.: Taboose Pass Trail, headwaters of South Fork Kings River, Kings Canyon National Park, *Shevock 13871*; Inyo Co.: trail from Onion Valley to Robinson Lake, Inyo National Forest, *Norris 46615*; Siskiyou Co.: trail from Cedar Lake to Cliff Lake, *Norris 52989* and Parks Creek at Forest Road 17, Shasta-Trinity National Forest, *Norris & Hillyard 104052*; Trinity Co.: Big Flat, *Norris 8930*.

****Campylopodiella stenocarpa* (Wilson in Seemann) P. Müller & Frahm** [Dicranaceae]

Illustrations: As *Atractyllocarpus stenocarpus* Sharp et al. 1994.

Geographic subdivisions: SN.

Selected specimens: Tulare Co.: Lion Meadows Creek near Little Kern River, Golden Trout Wilderness, Sequoia National Forest, *Norris 67935* (determined by Frahm).

***Campylopus introflexus* (Hedwig) Bridel**
[Dicranaceae]

Literature: Frahm 1980; O'Brien 1999; Shevock and Toren 2001; Showers 1982.

Illustrations: Frahm 1985; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SW.

Selected specimens: Humboldt Co.: three miles north of Manila on stabilized dunes, *Montalvo s.n.* (UC), Golf Course Road about 0.25 mile west of

Club House, Bayside Golf Course, *Norris* 53102; Lake Co.: south shore Clear Lake at Sulfur Bank Mine, *Toren* 8027 (CAS); Marin Co.: Limantour Beach, Point Reyes National Seashore, *O'Brien* 3353 (UC); Mendocino Co.: end of Simpson Land, Pygmy Cypress Forest, *Showers & Toren* 3258 (UC) [determined by Frahm] and Little River, Fern Canyon, *He* 40001 (MO); Monterey Co.: Cortez Road near Viscaino Road near Pebble Beach, *Yadon s.n.* (UC); San Francisco Co.: Mt. Davidson, *Toren* 7760 (CAS) [determined by Frahm]; San Mateo Co.: Pacifica, San Pedro County Park, *Bourell* 7000 (CAS); Santa Barbara Co.: Los Sauces Trail, Santa Cruz Island, Channel Islands National Park, *Robertson* 2154 (CAS); Shasta Co.: Boiling Springs Lake, Lassen Volcanic National Park, *Showers* 1909 (UC) [determined by Frahm].

***Campylopus pyriformis* (F. Schultz) Bridel**
[Dicranaceae]

Literature: Shevock and Toren 2001.

Illustrations: Arts and Frahm 1990; Smith 1978.

Geographic subdivisions: CW.

Selected specimens: San Francisco Co.: lawn area at Embarcadero near Piers 29 and 31, *Shevock* 19102 (determined by Frahm).

***Campylopus schmidii* (C. Müller Hal.) A. Jaeger** [Dicranaceae]

Literature: Christy and Wagner 1996. As *Campylopus aureus* Frahm 1980, 1985. As *Campylopus atrovirens* Holmberg 1969.

Illustrations: Frahm 1980, 1985.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: Stony Creek Trail near Gasquet, Six Rivers National Forest, *Nelson* 93 (UC), Gasquet, *Schofield* 28813 (MICH), bog about 2 miles north of Gasquet, Six Rivers National Forest, *Norris* 8167; Humboldt Co.: Big Lagoon north of Patricks Point State Park, *Bourell* 2005 (CAS, MO); Mendocino Co.: Pygmy Cypress Forest along Summers Road east of Fort Bragg, *Norris* 23457 & 23462 (determined by Frahm).

***Campylopus subulatus* W. P. Schimper in Rabenhorst** [Dicranaceae]

Literature: Frahm 1994; Kellman 2003; Shevock and Toren 2001.

Illustrations: Smith 1978.

Geographic subdivisions: CaR, CW, NW.

Selected specimens: Del Norte Co.: Stony Creek about 1 mile north of junction with Smith River, *Norris* 52767 (determined by Frahm) and French Hill Road about 3.5 miles above Highway 199 southeast of Gasquet, Six Rivers National Forest, *Norris* 85055 (MO); San Francisco Co.: Mt. Davidson, *Shevock* 19291 and Panhandle of Golden Gate Park, *Shevock* 18887 (determined by Frahm); Santa Cruz Co.: Scotts Valley, *Kellman* 1123 (CAS); Shasta Co.: Dry Creek Road at first bridge off of Highway 36 northeast of Redding, *Norris* 72342, 3.7 km east of Anderson, *Norris* 47645 (de-

termined by Frahm) and Sacramento River Trail northeast of Redding, *Norris* 105298.

***Ceratodon purpureus* (Hedwig) Bridel**
[Ditrichaceae]

Literature: Bourell 1981; Bradshaw 1926; Crum and Anderson 1981; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Long 1978; McCleary 1972; McGrew 1976; Mishler 1978; Sayre 1940; Shevock and Toren 2001; Showers 1982; Smith 1970; Spjut 1971; Steere 1954; Steere et al. 1954; Strid 1974; Toren 1977; Watson 1880; Whittemore and Sommers 1999; Yurky 1990. As *Ceratodon purpureus* var. *xanthopus* Lesquereux 1868; Sullivant 1856; Watson 1880.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Ochrya 1998a; Sharp et al. 1994; Smith 1978; Zander and Ireland 1979.

Geographic subdivisions: CaR, CW, GV, MP, NW, SN, SNE, SW.

Selected specimens: Butte Co.: levee of Feather River north of Gridley, *Norris* 52540; Modoc Co.: near Mayfield Ice Caves (Siskiyou Co.), *Norris & Hermann* 22519; San Diego Co.: Cameron Station Campground, Cleveland National Forest, *Norris* 57804; San Francisco Co.: Twin Peaks, San Francisco, *Shevock* 18862 & 19142; Sonoma Co.: South Ridge Trail above Lake Sonoma at Skaggs Springs Road, *Norris* 86938; Tulare Co.: Chamise Flats along Kern River 2.3 miles south of Roads End, Sequoia National Forest, *Shevock, Norris, & Barahona* 13028.

***Ceratodon stenocarpus* Bruch & W. P. Schimper** [Ditrichaceae]

Literature: Kellman 2003.

Illustrations: Burley and Prichard 1990; Sharp et al. 1994.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Mariposa Co.: Road to Mariposa Grove near Wawona Entrance Station, Yosemite National Park, *Shevock* 21434; Monterey Co.: Cemetery on Lockwood Road about 2 km east of Alamo Air Strip, Hunter-Liggett Military Reservation, *Norris* 87334 and Fish & Game Office on Garden Road, *Lind s.n.* (CAS) [determined by Robinson]; Santa Barbara Co.: Orcutt Hill, *Bratt s.n.* (SBBG); Santa Cruz Co.: Mount Hermon Road near Felton, *Kellman* 2803 (CAS); Shasta Co.: Mill Creek Road at Boulder Creek Trail, Whiskeytown National Recreation Area, *Norris & Hillyard* 105365; Tehama Co.: Highway 36 at Georgie Dells Road, *Norris* 56067.

***Claopodium bolanderi* Best** [Leskeaceae]

Literature: Bourell 1981; Holmberg 1969; Koch 1950a, 1951e; Lawton 1971; McGrew 1976; Noguchi 1964; Showers 1982; Spjut 1971; Toren 1977; Yurky 1990, 1995.

Illustrations: Lawton 1971; Noguchi 1964.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Del Norte Co.: Whiskey Lake, Six Rivers National Forest, *Norris* 83372; Humboldt Co.: South Fork Tish-Tang-a-Tang Creek east of Hoopa, *Norris & Whittemore* 52367; Lake Co.: Mt. Sanhedrin, *Shevock, Ertter, Toren, & Dearing* 19492; Marin Co.: Sir Francis Drake Blvd. Near Lagunitas, *Yurky* 402 (SFSU); Placer Co.: Bowman Lake west of Truckee, Tahoe National Forest, *Norris* 76955; Shasta Co.: Castle Lake at Castle Lake Creek, southwest of Mt. Shasta City, Shasta-Trinity National Forest, *Norris & Hillyard* 103845; Siskiyou Co.: Scotts Camp Creek Basin, *Norris* 53077; Tuolumne Co.: Forest Road 3N01 at Clavey Creek, Stanislaus National Forest, *Norris* 78792.

***Claopodium crispifolium* (W. J. Hooker)**

Renauld & Cardot [Leskeaceae]

Literature: Bourell 1981; Holmberg 1969; Jamieson 1969; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Noguchi 1964; Spjut 1971; Yurky 1990, 1995. As *Hypnum crispifolium* Sullivant 1856; Watson 1880.

Illustrations: Lawton 1971; Noguchi 1964.

Geographic subdivisions: CaR, CW, NW.

Selected specimens: Del Norte Co.: South Fork Smith River about 3 miles from Big Flat, *Norris* 74237; Marin Co.: Cataract Trail near Alpine Lake, *Yurky* 403 (SFSU); Mendocino Co.: Fox Creek, Branscomb Reserve, *Norris* 47188; San Mateo Co.: Pilarcitos Canyon below Lake Pilarcitos, *Steere s.n.* (UC); Shasta Co.: Damnation Pass Road at Lunch Gulch, *Norris & Hermann* 22563; Trinity Co.: Highway 36 at Clear Creek about 3 miles west of Forest Glen, *Norris* 68729.

***Claopodium whippleanum* (Sullivant) Renauld**

& Cardot [Leskeaceae]

Literature: Best 1897; Bourell 1981; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Long 1978; McCleary 1972; Mishler 1978; Noguchi 1964; Sayre 1940; Shevock and Toren 2001; Showers 1982; Sigal 1975; Smith 1970; Steere 1954; Steere et al. 1954; Thomson and Ketchledge 1958; Toren 1977; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Claopodium leuconeuron* Bradshaw 1926; Howe 1896; Kingman 1912; Millspaugh and Nuttall 1923. As *Claopodium whippleanum* var. *leuconeuron* McCleary 1972. As *Hypnum whippleanum* Sullivant 1856; Watson 1880.

Illustrations: Lawton 1971; Noguchi 1964; Sharp et al. 1994.

Geographic subdivisions: CaR, CW, DMoj, NW, SN, SW.

Selected specimens: Riverside Co.: Deep Springs Trail, San Jacinto State Park, San Jacinto Mountains, *Harpel* 554 (pers. herb.); San Bernardino Co.:

Kingston Peak, Kingston Wilderness, Mojave Desert, *Laeger & Bogan* 1765 (CAS); San Francisco Co.: Mt. Davidson, *Shevock* 19297; Santa Barbara Co.: Windmill Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock* 20904; Siskiyou Co.: Soda Creek about 4 miles northeast of Interstate 5 near Dunsmuir, Shasta-Trinity National Forest, *Norris* 84804; Sonoma Co.: Hamilton Ranch, 1 mile from Old Adobe east of Petaluma, *Koch* 337 (UC); Tulare Co.: General's Highway, 2.1 miles above Potwisha Campground and 0.2 miles below Hospital Rock, Middle Fork Kaweah River, Sequoia National Park, *Shevock* 15180.

***Conardia compacta* (C. Müller Hal.) H.**

Robinson [Campylaceae]

Literature: Ireland 1982. As *Amblystegium compactum* Cheney 1897; Flowers 1973; Koch 1950a; Koch and Ikenberry 1954; Lesquereux 1868; Steere 1954. As *Rhynchostegiella compacta* Harthill et al. 1979; Lawton 1971; Long 1978; McCleary 1972.

Illustrations: Flowers 1973; Hedenäs 1989a, 1993a, 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: DMoj, DSon, NW, SN, SNE, SW.

Selected specimens: Inyo Co.: Pine Creek Trail less than 0.5 mile from end of Pine Creek Road, Inyo National Forest, *Shevock, Halford, & Nelson* 15308; Lake Co.: along road to Harlin Springs south of Boggs Mountain, *Toren & Dearing* 7281 (CAS); Mariposa Co.: Highway 49 above Hells Hollow near milepost 32, *Shevock* 18749; Siskiyou Co.: Shasta Springs, *Howe* 127 (UC); Tulare Co.: Coy Flat Road, 0.25 mile south of bridge crossing of Middle Fork Tule River below Camp Nelson, Sequoia National Forest, *Norris, Shevock, & Barahona* 87663 & 87679; Ventura Co.: road to summit of Mt. Pinos about 1 mile below Chula Vista Campground, Los Padres National Forest, *Laeger* 1718 (CAS).

****Conostomum tetragonum* (Hedwig) Lindberg**

[Bartramiaceae]

Illustrations: Crum and Anderson 1981; Smith 1978.

Geographic subdivisions: SN, SNE.

Selected specimens: Alpine Co.: near Winnemucca Lake, Mokelumne Wilderness, Eldorado National Forest, *Norris* 71243; Mono Co.: Conness Lakes, Inyo National Forest, *Janeway* 7703 (UC).

***Coscinodon calypttratus* (Drummond) C. E. O.**

Jensen in Kindberg [Grimmiaceae]

Literature: Hastings 1999; Yurky 1995. As *Grimmia calypttrata* Flowers 1973; Harpel 1980a; Harthill et al. 1979; Koch 1950a; Lawton 1971; Lesquereux and James 1884; Spjut 1971.

Illustrations: Flowers 1973; Hastings 1999; Lawton 1971; Muñoz 1998c.

Geographic subdivisions: DMoj, MP, SNE, SW.

Selected specimens: Amador Co.: about 3 miles

west of Salt Springs Reservoir, Eldorado National Forest, *Norris & Shevock 103258*; Lassen Co.: Highway 139, 3 miles north of Susanville, *Whittemore 731a* (confirmed by Muñoz), and Termo-Grasshopper Road about 12 miles west of Termo, *Norris 22640*; Inyo Co.: on road to Schulman Grove, Ancient Bristlecone Pine Forest Botanical Area, White Mountains, Inyo National Forest, *Norris 46854*; Modoc Co.: Middle Alkali Lake north-east of Cedarville, *Norris 47496*, North Fork Pit River about 12 miles south of Davis Creek, *Norris 23624* and low hills north of Adin, *Norris 47421*; Riverside Co.: Highway 243 at milepost 10.77, San Jacinto Mountains, San Bernardino National Forest, *Harpel 87* (pers. herb.).

***Cratoneuron filicinum* (Hedwig) Spruce**
[Cratoneuraceae]

Literature: Harpel 1980a; Harthill et al. 1979; Koch 1949a, 1950a, 1958; Koch and Ikenberry 1954; Lawton 1971; Long 1978; Mishler 1978; Showers 1982; Spjut 1971; Strid 1974.

Illustrations: Flowers 1973; Hedenäs 1993a, 2003; Ireland 1982; Koponen et al. 1995; Lawton 1971; Ochya 1989; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, DMoj, MP, NW, SN, SNE, SW.

Selected specimens: Fresno Co.: Redwood Creek above Highway 180, Monarch Wilderness, Sequoia National Forest, *Shevock & York 12682* (determined by Ochya); Lake Co.: headwaters of Bear Creek, Snow Mountain Wilderness, Mendocino National Forest, *Toren & Dearing 7490* (CAS); Los Angeles Co.: Dorr Canyon northwest slope of Mt. Burham, Angeles National Forest, *Wheeler 8829 & 8830* (CAS, UC) [determined by Hedenäs]; Mono Co.: Koenig Lake near Leavitt Lake east of Sonora Pass, Toiyabe National Forest, *Norris 57209*; Nevada Co.: Sagehen Creek Biological Station, Tahoe National Forest, *Tavares 1965* (UC); Trinity Co.: above Big Boulder Lake west of Carrville, Shasta-Trinity National Forest, *Norris & Streimann 74842*; Tulare Co.: Deep Creek, Little Kern River, Golden Trout Wilderness, Sequoia National Forest, *Norris 67881*.

***Crossidium aberrans* Holzinger & E. B. Bartram** [Pottiaceae]

Literature: Flowers 1973; Kellman 2003; Lawton 1971; Stark and Whittemore 1992.

Illustrations: Delgadillo 1975; Dirkse and Bouman 1995; Flowers 1973; Lawton 1971; Sharp et al. 1994; Zander 1993.

Geographic subdivisions: CW, DMoj, DSon, GV, SW.

Selected specimens: Imperial Co.: about 2 miles east of Mountain Springs County Park, Colorado Desert, *Norris & Piippo 82086*; Inyo Co.: Fall Canyon, Grapevine Mountains, Death Valley National Park, *Laeger 834* (CAS); Kern Co.: Mesquite Canyon northwest of Garlock, El Paso Mountains, Mojave Desert, *Norris 87134*; Blunt-nosed Leopard

Lizard Preserve, San Joaquin Valley, *Shevock 10268*; Monterey Co.: Arroyo Seco Creek about 4 miles west of Greenfield, *Norris 48509*; San Diego Co.: canyon above Bow Willow Canyon Camp-ground, Anza Borrego State Park, *Norris 77723* and Sentenac Canyon along San Felipe Creek, 3.5 miles east of Scissors Crossing along Highway 78, *Stark 472c* (MO) [determined by Delgadillo].

***Crossidium crassinerve* (De Notaris) Juratzka**
[Pottiaceae]

Literature: As *Crossidium desertorum* Flowers 1973; Harthill et al. 1979; Koch 1950a; McCleary 1972; Sayre 1940.

Illustrations: Cano et al. 1992; Crum and Anderson 1981; Delgadillo 1975; Dirkse and Bouman 1995; Flowers 1973; Zander 1993.

Geographic subdivisions: CW, DMoj, DSon, GV, SN, SW.

Selected specimens: Fresno Co.: Pine Flat Reservoir near Trimmer, Sierra National Forest, *Norris 50942*; Imperial Co.: end of Clark Lane south of Coyote Wells, Colorado Desert, *Norris & Piippo 82072*; Inyo Co.: near Scottys Castle, Grapevine Mountains, Death Valley National Park, *Shevock 21334*; Kern Co.: Mesquite Canyon northwest of Garlock, El Paso Mountains, Mojave Desert, *Norris 87149* and Kern River along Highway 178, Sequoia National Forest, *Norris 50769*; San Luis Obispo Co.: about 1 mile west of Poso Summit, *Norris 55209*.

***Crossidium seriatum* H. Crum & W. C. Steere**
[Pottiaceae]

Literature: Stark and Whittemore 1992; Zander 1977b.

Illustrations: Crum and Steere 1958; Zander 1993.

Geographic subdivisions: DMoj, DSon, GV, SN, SW.

Selected specimens: Inyo Co.: Trail Canyon, Pan-amint Mountains, Death Valley National Park, *York 2342* (CAS); Kern Co.: about 2 miles east of Lost Hills adjacent to Interstate 5 and about 200 m southeast of junction with Highway 46, *Taylor 14747* (UC); Riverside Co.: road to Twentynine Palms about 8 miles west of Desert Center, *Norris 57932*; San Diego Co.: Santa Margarita Ecological Reserve, SDSU, *Kellman 1395 & 1400* (CAS); Tulare Co.: Elk Creek near Potwisha Campground, Sequoia National Park, *Norris, Shevock, & Barahona 87574*; road to Buckeye Campground, Sequoia National Park, *Norris, Shevock, & Barahona 87604*.

***Crossidium squamiferum* (Viviani) Juratzka**
[Pottiaceae]

Literature: Kellman 2003; Koch 1950a. As *Barbula chloronotos* Lesquereux 1868; Watson 1880. As *Crossidium griseum* Flowers 1973; Koch 1950a. As *Crossidium squamiferum* var. *pottioideum* Harpel 1980a; Harthill et al. 1979; Toren 1977. As *Tortula membranifolia* Coville 1893.

Illustrations: Delgadillo 1975; Dirkse and Bouman 1995; Flowers 1973; Ignatov and Ignatova 2003; Sharp et al. 1994; Zander 1993.

Geographic subdivisions: CW, DMoj, DSon, NW, SN, SNE, SW.

Selected specimens: Contra Costa Co.: Donner Canyon, Mt. Diablo State Park, *Shevock & Ertter* 20332; Fresno Co.: Warthan Creek about 7 miles west southwest of Coalinga, *Norris* 55132; Inyo Co.: Eco Canyon west of Inyo Mine, Death Valley National Park, *York* 2496 (CAS); Kern Co.: Mesquite Canyon northwest of Garlock, El Paso Mountains, Mojave Desert, *Norris* 87143; Riverside Co.: Highway 74 at Bighorn Overlook, San Bernardino National Forest, *Norris* 57853; San Diego Co.: Borrego Palm Canyon, Anza Borrego State Park, Colorado Desert, *Norris* 50571; Trinity Co.: Highway 299 about 1 mile east of Del Loma, Shasta-Trinity National Forest, *Norris* 70691; Tulare Co.: Elk Creek near Potwisha Campground, Sequoia National Park, *Norris, Shevock, & Barahona* 87577; Ventura Co.: above Blue Rocks Springs, *Norris* 55429, 55437, 55440, & 55447.

***Crumia latifolia* (Kindberg) W. B. Schofield** [Pottiaceae]

Literature: Bourell 1981; Christy and Wagner 1996; Harthill et al. 1979; Long 1978; Mishler 1978; Schofield 1966a; Shevock and Toren 2001; Toren 1977; Yurky 1990, 1995. As *Merceya latifolia* Koch 1950a; Koch and Ikenberry 1954; Moxley 1928; Thomson and Ketchledge 1958. As *Scopelephila latifolia* Flowers 1973; Lawton 1971.

Illustrations: Flowers 1973; Lawton 1971; Schofield 1966a; Zander 1993.

Geographic subdivisions: CaR, CW, DMoj, DSon, NW, SN, SNE, SW.

Selected specimens: Butte Co.: near Bidwell Bar, Feather River, *Schofield* 23138 (MO); Humboldt Co.: Tish-Tang Campground south of Hoopa, *Norris* 47305; Kern Co.: Cache Creek east of Horse Canyon, southern Piute Mountains, *Shevock & Hare* 14909; Los Angeles Co.: Twin Falls at La Cienega Camp North Fork San Gabriel Canyon north of Azusa, Angeles National Forest, *F. & R. Drouet* 3471 (UC); San Bernardino Co.: Caruthers Canyon, New York Mountains, Mojave National Preserve, *Laeger & Davis* 1334 (CAS); Santa Barbara Co.: canyon about 1 mile south of Bates Canyon Campground, Los Padres National Forest, *Norris* 55380; Santa Clara Co.: Stevens Canyon Road just east of Eden Canyon Road junction, *Whittemore* 5110 (MO); Trinity Co.: Highway 36 about 4 miles east of Wildwood, Shasta-Trinity National Forest, *Norris* 73561.

****Cynodontium jenneri* (W. P. Schimper in Howie) Stirton** [Dicranaceae]

Illustrations: Lawton 1971; Nyholm 1987–1998; Smith 1978.

Geographic subdivisions: SN.

Selected specimens: Madera Co.: Miller Meadow

below Minarets Pack Station, Sierra National Forest, *Norris & Hillyard* 105543.

****Cynodontium tenellum* (Bruch & W. P. Schimper) Limpricht** [Dicranaceae]

Illustrations: Ignatov and Ignatova 2003; Lawton 1971.

Geographic subdivisions: SN.

Selected specimens: Tulare Co.: Paradise Creek Trail near Buckeye Campground, Middle Fork Kaweah River, Sequoia National Park, *Shevock* 15191.

***Dacryophyllum falcifolium* Ireland** [Hypnaceae]

Literature: Ireland 2004.

Illustrations: Ireland 2004.

Geographic subdivisions: CW.

Selected specimens: Monterey Co.: Old Coast Road near South Fork Little Sur River, El Sur Ranch, *Kellman* 3037 (CAS); Santa Cruz Co.: South Fork Fall Creek from Blue Cliff above Lime Kilns. Henry Cowell Redwoods State Park, *Kellman* 704 (CAS) and Empire Grade at Cave Gulch, U.C. Santa Cruz property, *Kellman & Shevock* 2671 (CAS).

***Dendroalsia abietina* (W. J. Hooker) E. Britton in Brotherus** [Cryphaeaceae]

Literature: Bourell 1981; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Long 1978; Manuel 1974; Mishler 1978; Showers 1982; Smith 1970; Spjut 1971; Thomson and Ketchledge 1958; Toren 1977; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Alsia abietina* Bradshaw 1926; Lesquereux 1868; Moxley 1928; Watson 1880. As *Alsia circinalis* Kingman 1912. As *Leptodon circinatus* Sullivant 1856.

Illustrations: Brotherus 1924–1925; Lawton 1971; Manuel 1974; Sharp et al. 1994; Sullivant 1856.

Geographic subdivisions: CaR, CW, NW, SN, SW.

Selected specimens: Del Norte Co.: Smith River along Highway 199 about 9 miles east of junction with Highway 101, Six Rivers National Forest, *Norris* 85025; El Dorado Co.: Highway 50 at Ice House Road, *Norris & Piippo* 82284; Santa Barbara Co.: near Bates Canyon Campground, *Norris* 55378; Santa Cruz Co.: Pine Mountain Trail, Big Basin Redwoods State park, *Kellman* 2510 (CAS); Siskiyou Co.: near Cook and Green Pass about 1 mile west of White Mountain, Klamath National Forest, *Norris* 50187; Tulare Co.: trail below Crystal Cave to Cascade Creek, Sequoia National Park, *Shevock, Whitmarsh, & Johnson* 17168.

****Dichelyma uncinatum* Mitten** [Fontinalaceae]

Illustrations: Lawton 1971; Welch 1960.

Geographic subdivisions: NW.

Selected specimens: Mendocino Co.: Outlet Creek about 2 miles south of Willits, *Norris* 67593, Little Outlet Creek Bridge at Highway 101 about 5 miles north of Willits, *Duell* 680 (UC).

***Dichodontium flavescens* (Dickson) Lindberg**

[Dicranaceae]

Literature: Howe 1897.**Illustrations:** Werner 2002.**Geographic subdivisions:** SN, SNE.

Selected specimens: Alpine Co.: Silver Creek at Carson River, Toiyabe National Forest, *Norris* 78978; El Dorado Co.: South Fork American River, Highway 50 at Bridal Veil Falls, Eldorado National Forest, *Norris* 58415; Fresno Co.: Redwood Creek, Windy Gulch Grove, Sequoia National Forest, *Norris, Shevock, & York* 87947, 87951 and Dinkey Creek, Sierra National Forest, *Norris* 88208; Inyo Co.: Lone Pine Creek east of Movie Road, along Whitney Portal Road, *Norris & Shevock* 92912; Tulare Co.: near Atwell Mills Campground, East Fork Kaweah River, Sequoia National Park, *Norris* 46431 and Slate Mountain Botanical Area near junctions of Forest Trails 31E14 and 31E31, Sequoia National Forest, *Shevock* 15693.

***Dichodontium olympicum* Renauld & Cardot**

[Dicranaceae]

Illustrations: Lawton 1971.**Geographic subdivisions:** CaR, NW, SN, SNE.

Selected specimens: Mono Co.: Lundy Lakes Trail along Mill Creek below Lake Helen, Inyo National Forest, *Norris* 78864, 78887 & 78890; Siskiyou Co.: between Louise, O'Brien and Eastern Creeks on eastern slopes of Little Grayback, *Holmberg* 947 (UC); Tuolumne Co.: about 2 miles east of Tuolumne Meadows toward Tioga Pass, Yosemite National Park, *Norris* 100356.

Dichodontium pellucidum* (Hedwig) W. P.*Schimper** [Dicranaceae]

Literature: Bourell 1981; Crum and Anderson 1981; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Long 1978; Showers 1982; Spjut 1971; Strid 1974; Tan and Schofield 1980; Thomson and Ketchledge 1958; Toren 1977.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Smith 1978; Werner 2002.

Geographic subdivisions: CaR, CW, MP, NW, SN, SW.

Selected specimens: Alpine Co.: Silver Creek at Carson River, Toiyabe National Forest, *Norris* 78978; Fresno Co.: Avalanche Creek at Cedar Grove, South Fork Kings River, Kings Canyon National Park, *Shevock* 13770; Humboldt Co.: Forest Road 5E21 at East Fork about 5 air miles north of Mad River, Six Rivers National Forest, *Norris* 83887; Lake Co.: beyond Towhead Flat, Mt. Sanhedrin, Mendocino National Forest, *Toren* 5077 (CAS); Riverside Co.: Middle Spring along Devils Slide Trail, San Jacinto Mountains, San Bernardino National Forest, *Harpel* 941 (pers. herb.); Shasta Co.: Highway 299 north side of Haynes Flat about

3 miles west of Burney, *Norris* 68563; Siskiyou Co.: Shadow Creek at Callahan about 6 miles northeast of Cecilville, Klamath National Forest, *Norris* 70552.

***Dicranella crispa* (Hedwig) W. P. Schimper**

[Dicranaceae]

Illustrations: Ignatov and Ignatova 2003; Lawton 1971; Smith 1978.

Geographic subdivisions: NW.

Selected specimens: Siskiyou Co.: mouth of West Fork Clear Creek, Siskiyou Mountains, Klamath National Forest, *Wheeler* 8281 (CAS, UC).

Dicranella heteromalla* (Hedwig) W. P.*Schimper** [Dicranaceae]

Literature: Crum and Anderson 1981; Howe 1897; Jamieson 1969; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Shevock and Toren 2001; Yurky 1990, 1995. As *Dicranum heteromallum* Lesquereux 1868; Watson 1880.

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CW, NW.

Selected specimens: Del Norte Co.: trail between Requa and False Klamath Cove, Redwood National Park, *Norris* 24029 and Sanger Lake, Six Rivers National Forest, *Norris* 7773 & 7775; Glenn Co.: Cottonwood Glade east of Plaskett Meadows, Mendocino National Forest, *Norris* 47961; Humboldt Co.: Goose Creek, *Norris* 56531; Marin Co.: South Novato, *Jenkinson s.n.* (UC); Mendocino Co.: east of Highway 1 just south of Caspar, Pygmy Cypress Forest, *Tavares & Sharsmith* 732 (UC); San Francisco Co.: Mt. Davidson, *Shevock* 18928; Santa Cruz Co.: Waddell Creek near Redwoods Camp 2, Big Basin Redwoods State Park, *Kellman* 782 (CAS); Sonoma Co.: Bodega Marine Laboratory, *Norris* 103450.

***Dicranella hilariana* (Montagne) Mitten**

[Dicranaceae]

Illustrations: Crum and Anderson 1981; Grout 1928–1940; Sharp et al. 1994. As *Dicranum debile* Cardot and Thériot 1900; Sullivan 1864.

Geographic subdivisions: CW.

Selected specimens: Santa Cruz Co.: City of Capitola, *Kellman* 1052 (CAS) [determined by Frahm].

***Dicranella howei* Renauld & Cardot**

[Dicranaceae]

Literature: Cardot and Thériot 1900; Crundwell and Nyholm 1977; Howe 1896; Kellman 2003; Shevock and Toren 2001; Whitmore and Sommers 1999. Misapplied as *Anisothecium varium* Koch 1950a; Koch and Ikenberry 1954; Steere 1954; Steere et al. 1954. Misapplied as *Dicranella varia* Bourell 1981; Bradshaw 1926; Crum and Anderson 1981; Harpel 1980a; Harthill et al. 1979; Jamieson 1969; Lawton 1971; McCleary 1972; Mishler 1978; Sayre 1940; Shevock and Toren 2001; Toren 1977;

Yurky 1990, 1995. Misapplied as *Dicranum varium* Lesquereux 1868; Watson 1880. As *Dicranella rubra* Millspaugh and Nuttall 1923. As *Dicranum palustre* Lesquereux 1868.

Illustrations: Crundell and Nyholm 1977; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Butte Co.: opposite spillway of Oroville Dam, *Norris* 52580; Fresno Co.: Peterson Mill Road at junction with Forest Roads 10S18 & 10S43, about 6 miles east of Highway 168, Sierra National Forest, *Shevock & York* 14970; Humboldt Co.: Humboldt Bay at foot of L Street, Eureka, *Norris* 57794; Lake Co.: Erickson Ridge Road to Mt. Sanhedrin, Mendocino National Forest, *Toren* 5085 (CAS); Nevada Co.: Washington Road, 2.7 miles from Highway 20, Tahoe National Forest, *Shevock & Toren* 20713; San Francisco Co.: Coastal Bluff Trail, Golden Gate National Recreation Area, *Shevock* 18806; Santa Cruz Co.: Eagle Creek below Columbine Trail Crossing, Henry Cowell Redwoods State Park, *Kellman* 631 (CAS).

****Dicranella pacifica* W. B. Schofield**

[Dicranaceae]

Illustrations: Lawton 1971.

Notes: See Schofield (1970) for a table of characters separating *D. pacifica* from *D. varia*.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: Bear Basin Butte, Six Rivers National Forest, *Norris* 8095.

****Dicranella palustris* (Dickson) Crundwell ex.**

Warburg [Dicranaceae]

Illustrations: Crum and Anderson 1981; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: NW.

Selected specimens: Siskiyou Co.: Long Gulch Lake southwest of Callahan, Klamath National Forest, *Norris* 57476.

****Dicranella rufescens* (Withering) W. P.**

Schimper [Dicranaceae]

Illustrations: Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971.

Geographic subdivisions: NW, SN.

Selected specimens: Calaveras Co.: about 1 mile west of Salt Springs Reservoir, Stanislaus National Forest, *Norris & Shevock* 103254; Lake Co.: Library Park, City of Lakeport, *Toren* 8430 (CAS) and *Toren & Shevock* 8514 (CAS) [determined by Allen]; Mendocino Co.: location not specified beyond T12N, R13W, sections 21–23, *Hamilton* 87 (UC).

****Dicranella schreberiana* (Hedwig) Hilfert ex**

H. Crum & Anderson [Dicranaceae]

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971.

Geographic subdivisions: NW.

Selected specimens: Humboldt Co.: slopes about 2.5 miles from Highway 299 at Redwood Valley,

Duell 1891 (UC) and above South Quarry Road off Jacoby Creek Road near Arcata, *Norris* 57660.

***Dicranella subulata* (Hedwig) W. P. Schimper**
[Dicranaceae]

Literature: Crum and Anderson 1981; Koch 1950a; Lawton 1971. As *Dicranum subulatum* Lesquereux 1868; Watson 1880.

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971.

Geographic subdivisions: NW.

Selected specimens: Humboldt Co.: Van Duzen River floodplain about 3 miles east of Carlotta, *Norris* 19604 and Salmon Creek Road about 3 miles above mouth of Salmon Creek, *Nomura & Kirn* 79 (UC).

***Dicranoweisia cirrata* (Hedwig) Lindberg in Milde** [Seligeriaceae]

Literature: Bourell 1981; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Kellman 2003; Kingman 1912; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux and James 1884; Long 1978; Mishler 1978; Moxley 1928; Shevock and Toren 2001; Showers 1982; Sigal 1975; Smith 1970; Spjut 1971; Steere et al. 1954; Toren 1977; Yurky 1990, 1995. As *Weissia cirrata* Lesquereux 1868; Sullivant 1856; Watson 1880.

Illustrations: Flowers 1956; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN, SW.

Selected specimens: Lake Co.: Clear Lake State Park, *Norris* 47731; Plumas Co.: forest campsite along Highway 24 and North Fork Feather River, *Koch* 1873 (UC); Riverside Co.: Riverside County Park near Idyllwild, San Jacinto Mountains, *Harpel* 1465 (pers. herb.); San Francisco Co.: Mt. Sutro, *Shevock* 19180; Santa Barbara Co.: Orcutt Hill, *Bratt s.n.* (SBBG); Santa Cruz Co.: Zayante Canyon Road about 4 miles south of Summit Road north of Felton, Santa Cruz Mountains, *Norris* 86868; Siskiyou Co.: Soda Creek Road about 4 miles northeast of Highway 5 near Dunsuir, Shasta-Trinity National Forest, *Norris* 84791; Tulare Co.: County Road M-220 at Bear Creek, Sequoia National Forest, *Norris*, *Shevock*, & *Barahona* 87651.

***Dicranoweisia contermina* Renauld & Cardot**
[Seligeriaceae]

Literature: Howe 1897; Koch 1950a. Misapplied in California as *Dicranoweisia crispula* Bradshaw 1926; Flowers 1973; Lesquereux and James 1884; Showers 1982; Spjut 1971; Strid 1974. As *Dicranoweisia crispula* var. *contermina* Holmberg 1969; Lawton 1971; McGrew 1976.

Notes: *Dicranoweisia crispula* has historically been reported for California, however, based on our examination of the specimens residing in California herbaria, we view these plants, primarily of rock outcrops, to be *Dicranoweisia contermina*. We ex-

pect *Dicranoweisia crispula* to be located within the Sierra Nevada. See Appendix III for more information.

Illustrations: Crum and Anderson 1981; Flowers 1956, 1973; Ireland 1982; Lawton 1971.

Geographic subdivisions: CaR, MP, NW, SN, SNE.

Selected specimens: Modoc Co.: Big Valley Mountains, *Baker & Nutting s.n.* (UC); Placer Co.: Bowman Lake Road at Grouse Mountain Road west of Truckee, Tahoe National Forest, *Norris 76983*; Siskiyou Co.: near Monument Lake, Marble Mountain Wilderness, Klamath National Forest, *Norris & Spjut 12453*; Trinity Co.: slopes above Lake Eleanor west of Trinity Center, *Norris 76881*; Tulare Co.: Crabtree Meadows near Mount Whitney, Sequoia National Park, *Shevock 18546*.

***Dicranum fuscescens* Turner** [Dicranaceae]

Literature: Bourell 1981; Crum and Anderson 1981; Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Shevock and Toren 2001; Showers 1982; Smith 1970; Spjut 1971; Toren 1977; Watson 1880; Yurky 1990, 1995.

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Del Norte Co.: Stony Creek about 1 mile north of Gasquet, Six Rivers National Forest, *Norris & Piippo 82459*; Humboldt Co.: Foothill Trail, Prairie Creek Redwood State Park, *Norris 46007*; Lake Co.: east slope of Garrett Mountain, Mendocino National Forest, *Toren 7171* (CAS); Mendocino Co.: Comptche Road about 3 miles east of Mendocino, Pygmy Cypress Forest, *Norris 10739* (determined by Peterson); Santa Cruz Co.: West Waddell Creek, Big Basin Redwoods State Park, *Kellman 2479* (CAS); Siskiyou Co.: near Cook and Green Pass about 1 mile west of White Mountain, Klamath National Forest, *Norris 50196*; Tuolumne Co.: Dodds, Strawberry Lake near Pinecrest, Stanislaus National Forest, *Morse 1934* (UC) [determined by Peterson].

***Dicranum howellii* Renauld & Cardot**

[Dicranaceae]

Literature: Bourell 1981; Howe 1896; Kellman 2003; Lawton 1971; Shevock and Toren 2001; Toren 1977. Misapplied as *Dicranum scoparium* Holmberg 1969; Jamieson 1969; Koch 1950a; Koch and Ikenberry 1954; Lesquereux 1868; Spjut 1971; Watson 1880; Yurky 1995. As *Dicranum bonjeanii* Holmberg 1969; Koch 1950a, 1951e; Spjut 1971; Yurky 1990.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Butte Co.: about 2 miles northeast of Forbestown, Plumas National Forest, *Dillingham 1011* (CAS) and arm of Oroville Lake near Bloomer Hill, *Janeway 7745* (UC); Del Norte

Co.: Whiskey Lake, Six Rivers National Forest, *Norris 83369*; Humboldt Co.: Emerald Creek east of Orick, *Norris 24591*; Mendocino Co.: Eel River about 3 miles south of Piercy, *Norris 72142*; San Francisco Co.: Mt. Davidson, *Shevock 19290*; Santa Cruz Co.: Whites Lagoon, Forest of Nisene Marks State Park, *Kellman 774* (CAS); Shasta Co.: Soda Creek Road about 3 miles northeast of Highway 5 near Dunsmuir, Shasta-Trinity National Forest, *Norris 84783*; Siskiyou Co.: Clear Creek below Young's Valley, *Norris & Ignatov 74747*; Trinity Co.: Hennessy Ridge Road about 1 mile west of eastern border of Six Rivers National Forest, *Norris 77269*.

***Dicranum scoparium* Hedwig** [Dicranaceae]

Literature: Lawton 1971.

Illustrations: Abramov and Volkova 1998; Ignatov and Ignatova 2003; Lawton 1971.

Notes: Although attributed to California in the bryological literature, all but one of the California specimens we examined labeled as *Dicranum scoparium* are actually *D. howellii*.

Geographic subdivisions: NW.

Selected specimens: Siskiyou Co.: Granite Creek between Tikner Creek and Blue Granite, *Norris 52329*.

****Dicranum sulcatum* Kindberg in Macoun**

[Dicranaceae]

Illustrations: Peterson 1979.

Geographic subdivisions: CaR, CW, NW.

Selected specimens: Del Norte Co.: Highway 199 at Elk Valley Campground near Oregon border, Siskiyou National Forest, *Norris 9848*; Humboldt Co.: Ten Taypo Trail, Prairie Redwoods State Park, *Norris 56794*; Marin Co.: trail near Mud Lake, Point Reyes National Seashore, *Norris 71828*; Mendocino Co.: about 5 miles east of Albion, Pygmy Cypress Forest, *Norris 11791* and Gibney Lane about 1.2 miles east of Highway 1 near Fort Bragg, *Becking s.n.* (UC); Siskiyou Co.: between Louise and Indian Creek, slopes of Little Grayback, Klamath National Forest, *Holmberg 948* (UC).

****Dicranum undulatum* Schrader ex Bridel**

[Dicranaceae]

Illustrations: Lawton 1971.

Notes: The occurrence of this species in California is viewed as a recent introduction that may spread to other areas in the San Francisco Bay Area.

Geographic subdivisions: CW.

Selected specimens: Alameda Co.: U. C. Berkeley Campus, Valley Life Sciences Building, *Kersh & Norris 4* (UC) and *Shevock 21626* (confirmed by Ireland).

***Didymodon australasiae* (W. J. Hooker & Greville) Zander** [Pottiaceae]

Literature: Shevock and Toren 2001. As *Trichostomopsis brevifolia* Bartram 1931; Harthill et al. 1979; Koch 1950a, 1951e; McCleary 1972; Steere

1954. As *Trichostomopsis diaphanobasis* Harthill et al. 1979. As *Trichostomopsis faye* Harthill et al. 1979; Koch 1950a; McCleary 1972; Steere 1954. As *Trichostomopsis australasiae* Lawton 1971.

Illustrations: Allen 2002; Bartram 1931; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: CW, DMOj, DSon, SW.

Selected specimens: Inyo Co.: Titus Canyon, Death Valley National Park, *Norris 10206f*; Kern Co.: Sand Canyon Road just north of Highway 58, *Shevock 13237*; Lake Co.: Chalk Mountain north of Cache Creek, *Toren & Dearing 7310* (CAS); Los Angeles Co.: San Fernando Valley, *MacFadden 21719* (MO); Riverside Co.: Snakeye Springs, Indian Cove, Joshua Tree National Park, *Norris 57992*; San Diego Co.: Box Canyon, Anza Borrego State Park, Colorado Desert, *Norris 50630*; San Francisco Co.: Golden Gate Park, *Shevock 18896* (determined by Zander); San Luis Obispo Co.: about 1 mile west of Poso Grade, *Norris 55215*; Tuolumne Co.: along Highway 120 about 5 miles below Jamestown, *Ikenberry 394* (MO) [determined by Grout].

***Didymodon brachyphyllus* (Sullivant in Whipple) Zander** [Pottiaceae]

Literature: Kellman 2003. As *Barbula brachyphylla* Harpel 1980a; Harthill et al. 1979; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Long 1978; McCleary 1972; Mishler 1978; Sayre 1940; Spjut 1971; Steere 1954; Steere et al. 1954; Sullivant 1856; Toren 1977; Watson 1880; Yurky 1990. As *Didymodon vinealis* var. *brachyphyllus* Yurky 1995.

Illustrations: Lawton 1971; Mogensen and Zander 1999; Sharp et al. 1994; Zander and Ochrya 2001.

Geographic subdivisions: CW, NW, SN, SNE, SW.

Selected specimens: Contra Costa Co.: Vasco Caves Preserve, East Bay Regional Parks, *Shevock, O'Brien, & Jessup 15025* (determined by Zander); Lake Co.: Highway 20 about 10 miles east of Highway 53 junction, *Toren & Dearing 7317* (CAS) [confirmed by Zander]; Marin Co.: Shell Beach Trail, *Yurky 325* (SFSU); Riverside Co.: Garnet Queen Creek, Santa Rosa Mountains, *Harpel 2355* (pers. herb.); San Diego Co.: French Creek, Palomar Mountains, *Stark 771* (MO); Tulare Co.: Highway 190 at Soda Creek near Moorehouse, Sequoia National Forest, *Shevock 15650* (determined by Zander); Ventura Co.: San Nicolas Island, *Weber & Bratt 100684* (MO).

***Didymodon eckeliae* Zander** [Pottiaceae]

Literature: Zander 2001.

Illustrations: Zander 2001.

Geographic subdivisions: SW.

Selected specimens: San Diego Co.: about 13 km northeast of Lakeside, Barona Indian Reservation, *Wiggins s.n.* (NY).

***Didymodon fallax* (Hedwig) Zander** [Pottiaceae]

Illustrations: Ignatov and Ignatova 2003. As *Barbula fallax* Crum and Anderson 1981; Lawton 1971; Smith 1978.

Geographic subdivisions: CW.

Selected specimens: Alameda Co.: Berkeley, *Morse s.n.* (NY); Santa Clara Co.: Big Basin Way, Highway 9 about 1 mile from Saratoga, *Duell 2148* (NY) [determined by Zander].

***Didymodon ferrugineus* (W. P. Schimper ex Bescherele) M. O. Hill** [Pottiaceae]

Illustrations: Allen 2002; Ignatov and Ignatova 2003.

Geographic subdivisions: CaR, NW.

Selected specimens: Siskiyou Co.: Mud Creek Dam along Forest Road 40N56, southeast slopes of Mt. Shasta, Shasta-Trinity National Forest, *Norris & Hillyard 104089*.

***Didymodon insulanus* (De Notaris) M. O. Hill** [Pottiaceae]

Literature: Shevock and Toren 2001. As *Barbula cylindrica* Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Kingman 1912; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lesquereux 1868; Lesquereux and James 1884; Long 1978; McCleary 1972; Mishler 1978; Sayre 1940; Steere 1954; Toren 1977; Yurky 1990, 1995. As *Barbula flexifolia* Brandegees 1891; Lesquereux and James 1884. As *Barbula insulana* Lesquereux 1868. As *Barbula subfallax* Brandegees 1891; Kingman 1912; Lesquereux 1868; Lesquereux and James 1884; Millspaugh and Nuttall 1923. As *Barbula virescens* Brandegees 1891; Lesquereux and James 1884. As *Didymodon vinealis* var. *flaccida* Lawton 1971; Whittemore and Sommers 1999; Yurky 1990, 1995.

Illustrations: Lawton 1971.

Geographic subdivisions: CW, SN.

Selected specimens: Alameda Co.: Little Yosemite Canyon View Trail, Sunol Regional Park, *Whittemore 5428b* (MO); El Dorado Co.: Bridal Veil Falls, Highway 50, Eldorado National Forest, *Whittemore 4000* (MO); San Mateo Co.: Sylvan Trail, Edgewood County Park, *Whittemore & Sommers 5259* (MO); Santa Cruz Co.: Rincon Gorge, Henry Cowell Redwoods State Park, *Kellman 363* (CAS); Tulare Co.: Belknap Grove near Camp Nelson, Middle Fork Tule River, Sequoia National Forest, *Norris 50902*.

***Didymodon nicholsonii* Culmann** [Pottiaceae]

Literature: Kellman 2003; Shevock and Toren 2001. As *Didymodon vinealis* var. *nicholsonii* Showers 1982.

Illustrations: Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN, SW.

Selected specimens: Alameda Co.: Little Yosemite Canyon View Trail, Sunol Regional Park, *Whittemore*

more 5452 (MO); Butte Co.: North Fork Feather River Canyon above Highway 70, Plumas National Forest, *Janeway 5370* (MO); Fresno Co.: Deer Cove Creek adjacent to Highway 180, South Fork Kings River, Sequoia National Forest, *Shevock 12457*; Lake Co.: near Lake Pillsbury, Mendocino National Forest, *Toren 7138a* (BUF, CAS) [confirmed by Zander]; Riverside Co.: Santa Rosa Mountain, *Norris 57875*; Santa Cruz Co.: Laguna Creek, *Kellman 1522* (CAS); Sonoma Co.: Wolf Creek Road about 4 miles east of Gualala River, *Norris 86944*.

***Didymodon norrisii* Zander** [Pottiaceae]

Literature: Kellman 2003; Zander 1999.

Illustrations: Zander 1999.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Contra Costa Co.: near Castle Rocks, Mt. Diablo State Park, *Shevock & Ertter 20347*; Humboldt Co.: near Kneeland, *Norris 7884* (BUF, UC); Lake Co.: Manning Creek, Highway 175 about 4 miles west of Lakeport, *Toren, Bourell, Dearing, & Shevock 6940* (CAS) and *Toren 7402* (CAS), Hell's Peak near Blue Lakes, *Toren 636* (CAS), The Slides west of Lake Pillsbury, Mendocino National Forest, *Toren 7534* (CAS) [determined by Zander], *Shevock, Ertter, Toren, & Dearing 19488*, and Bartlett Mountain Road at High Valley Ridge, Mendocino National Forest, *Norris 10606*; Madera Co.: Forest Highway 81 between Fish Creek and Slide Creek, Sierra National Forest, *Shevock & Norris 19785*; Nevada Co.: road to Downieville about 3 miles from Nevada City, *Norris 67384*; Santa Cruz Co.: Eagle Rock Lookout Tower near Bonny Doon, *Kellman 890* (CAS); Tehama Co.: Hogback Road about 4 miles east of Highway 99, *Shevock & Ertter 22251*; Tulare Co.: near Brush Creek along Kern River, Sequoia National Forest, *Toren 7936* (CAS); Tuolumne Co.: Highway 108 east of Long Barn, 6.1 miles east of Mi-Wok Ranger Station, Stanislaus National Forest, *Shevock 18586* (determined by Toren).

***Didymodon occidentalis* Zander** [Pottiaceae]

Literature: Whittemore and Sommers 1999. As *Barbula rubiginosa* Harthill et al. 1979; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Spjut 1971; Toren 1977.

Illustrations: Lawton 1971.

Geographic subdivisions: CW, NW, SN.

Selected specimens: Colusa Co.: Highway 20 at milepost 74, *Norris 52515, 52522, & 52526*; Contra Costa Co.: Mitchell Canyon, Mt. Diablo State Park, *Norris 100606*; Fresno Co.: Warthan Creek about 7 miles southwest of Coalinga, *Norris 55124*; Kern Co.: Round Mountain Road, 5.79 miles east of junction with Granite Road and 1.9 miles west of Eastmont Road, north of Oildale, *Shevock 14841*; San Luis Obispo Co.: near Black Mountain and Navajo Camp about 1.5 miles west of road junction, *Norris 55244*.

***Didymodon revolutus* (Cardot) R. S. Williams** [Pottiaceae]

Literature: As *Husnotiella revoluta* Bartram 1926; Grout 1928–1940; Harthill et al. 1979; Koch 1949a, 1950a; Koch and Ikenberry 1954.

Illustrations: Allen 2002; Crum and Anderson 1981; Sharp et al. 1994.

Geographic subdivisions: CW, MP, SN.

Selected specimens: Contra Costa Co.: Pine Canyon near Castle Rocks, Mt. Diablo State Park, *Norris 100792*; Lassen Co.: Highway 139 about 16 miles south of Adin, *Norris 21462 & 21466*; Modoc Co.: Alturas, North Fork Pit River, *Richards & Drouet 1263* (UC); Placer Co.: American River Canyon at junction of Highway 49 and Foresthill Road, *Whittemore 4339* (MO); San Luis Obispo Co.: Boy Scout Road about 1 mile east of Twin Bridges, Camp Roberts Military Reservation, *Norris 100885*; Sonoma Co.: Adobe Canyon, *Koch 285* (UC) and near Kenwood, *Koch s.n.* (MO) [determined by Bartram]; Tulare Co.: Limestone Campground, Kern River Canyon, Sequoia National Forest, *Norris, Shevock, & Barahona 87102*; Tuolumne Co.: about 5 miles below Jamestown, *Ikenberry 394* (CAS) [determined by Koch].

***Didymodon rigidulus* Hedwig** [Pottiaceae]

Literature: Bourell 1981; Flowers 1973; Kellman 2003; Lawton 1971; Shevock and Toren 2001; Sigal 1975; Yurky 1990, 1995. As *Barbula acuta* Koch 1950a; Lawton 1971. As *Barbula rigidula* Kingman 1912; Harthill et al. 1979; Koch 1950a; Long 1978; Watson 1880. As *Didymodon mexicanus* var. *subulatus* Harthill et al. 1979; McCleary 1972. As *Didymodon rigidulus* var. *icmadophilus* Zander 1981b, 1993. As *Trichostomum rigidulum* Lesquereux 1868; Lesquereux and James 1884; Moxley 1928.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978; Zander 1993.

Geographic subdivisions: CW, NW, SN, SW.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris 87188*; Fresno Co.: divide above Boyden Cave, Monarch Wilderness, Sequoia National Forest, *Shevock & York 12330* and Warthan Creek about 7 miles west southwest of Coalinga, San Joaquin Valley, *Norris 55135*; Lake Co.: Highway 53 about 1 mile south of Highway 20, *Norris 47687*; Marin Co.: Bootjack Trail, Mt. Tamalpais State Park, *Yurky 860* (SFSU); San Benito Co.: Clear Creek, San Benito Mountain, BLM Clear Creek Recreation Area, *Shevock, Norris, & Hamon 20303* (determined by Zander); San Bernardino Co.: Highway 40 about 15 miles east of Barstow, Mojave Desert, *Norris 68082*; San Diego Co.: Matagual Creek, Volcan Mountains, *Stark 611* (BUF); San Francisco Co.: Golden Gate Park, *Shevock 19515*; Siskiyou Co.: Elk Creek at Malone Creek south of Happy Camp, *Norris 52250*.

***Didymodon tophaceus* (Bridel) Lisa** [Pottiaceae]

Literature: Crum and Anderson 1981; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Kingman 1912; Koch 1950a; Lawton 1971; Long 1978; McCleary 1972; Millspaugh and Nuttall 1923; Mishler 1978; Shevock and Toren 2001; Sigal 1975; Steere 1954; Toren 1977; Yurky 1990, 1995. As *Desmatodon hendersonii* Koch 1950a; McCleary 1972; Millspaugh and Nuttall 1923; Steere 1954; Steere et al. 1954. As *Trichostomum tophaceum* Lesquereux 1868; Lesquereux and James 1884; Sullivant 1856; Watson 1880.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CW, DMOj, DSon, NW, SN, SNE, SW.

Selected specimens: Fresno Co.: just below bridge crossing of Highway 180 at Boyden Cave, Sequoia National Forest, *Shevock 12459*; Inyo Co.: Cottonwood Canyon, Cottonwood Mountains, Death Valley National Park, *Shevock, Kellman, York, & Knaus 20559*; Napa Co.: near Lake Berryessa about 4 miles east of Pope Valley, *Norris 48257*; Nevada Co.: Washington Road about 2.5 miles from Highway 20, Tahoe National Forest, *Shevock & Toren 20711*; Riverside Co.: Bay Tree Springs, San Jacinto Mountains, San Bernardino National Forest, *Harpel 1848* (pers. herb.); Santa Barbara Co.: La Jolla Vieja Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock & Rodriguez 20867*; Santa Clara Co.: Alum Rock Park, San Jose, *Schofield 12697* (UC); Siskiyou Co.: Sawyers Bar to Forks of the Salmon Road about 2 miles east of Forks of the Salmon, *Norris 22760*.

***Didymodon umbrosus* (C. Müller Hal.) Zander** [Pottiaceae]

Literature: Shevock and Toren 2001.

Illustrations: Eckel 1986; Sharp et al. 1994.

Geographic subdivisions: CW.

Selected specimens: San Francisco Co.: Aqua Vista Park, China Basin, San Francisco, *Shevock 18997* (determined by Zander).

***Didymodon vinealis* (Bridel) Zander** [Pottiaceae]

Literature: Kellman 2003; Koch and Ikenberry 1954; Shevock and Toren 2001; Showers 1982; Whittemore and Sommers 1999. As *Barbula bakeri* Cardot and Thériot 1904. As *Barbula semitorta* Kingman 1912; Lesquereux 1868; Lesquereux and James 1884; Sullivant 1856. As *Barbula vinealis* Bourell 1981; Bradshaw 1926; Brandege 1891; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Koch 1950a, 1951e; Lawton 1971; Lesquereux and James 1884; Long 1978; McCleary 1972; Millspaugh and Nuttall 1923; Mishler 1978; Moxley 1928; Sigal 1975; Smith 1970; Spjut 1971; Steere 1954; Steere et al. 1954; Sullivant 1856; Thomson and Ketchledge 1958; Toren 1977; Watson 1880. Probably misapplied as *Barbula arcto-*

carpa Millspaugh and Nuttall 1923; Lesquereux and James 1884. As *Tortula elata* Brandege 1891.

Illustrations: Allen 2002; Ignatov and Ignatova 2003; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, DMOj, DSon, GV, MP, NW, SN, SNE, SW.

Selected specimens: Fresno Co.: Marble Falls Trail above Potwisha Campground, Marble Fork Kaweah River, Sequoia National Park, *Shevock 12951*; Humboldt Co.: Forest Road 5E21 at East Fork about 5 air miles north of Mad River, Six Rivers National Forest, *Norris 83890*; Mariposa Co.: road to Big Sandy about 2 miles east of Fish Camp, Sierra National Forest, *Norris 85337*; Santa Barbara Co.: canyon about 1 mile south of Bates Canyon Campground, *Norris 55357*; Shasta Co.: County Road A17 at junction of road to Black Butte, *Norris 23746*; Tulare Co.: Dark Canyon along Forest Road 24S05 just south of White River Campground, Sequoia National Forest, *Shevock 14300* and Mineral King Road, 0.5 mile east of Silver City, Sequoia National Park, *Shevock 17665* (determined by Zander).

****Discelium nudum* (Dickson) Bridel** [Disceliaceae]

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Lawton 1971.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: between False Klamath Cove and Requa, Redwood National Park, *Norris 24047, 70386 & 70723*; Humboldt Co.: Patrick's Point near Arcata, *Schofield 16971* (UBC).

***Distichium capillaceum* (Hedwig) Bruch & W.**

P. Schimper [Ditrichaceae]

Literature: Crum and Anderson 1981; Koch 1949a, 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Showers 1982; Watson 1880.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Ochrya 1998a; Seppelt 1982; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, MP, NW, SN, SNE.

Selected specimens: Alpine Co.: Winnemucca Lake, Mokelumne Wilderness, Eldorado National Forest, *Norris 71269*; Inyo Co.: South Fork Bishop Creek, 4.2 miles south of Highway 168 on South Lake Road, Inyo National Forest, *Shevock 12546*; Modoc Co.: above Patterson Lake, South Warner Wilderness, Modoc National Forest, *Harpel 2271* (pers. herb.); Mono Co.: Lundy Lakes Trail below Helen Lake, Inyo National Forest, *Norris 78888*; Siskiyou Co.: Taylor Lake, Klamath National Forest, *Norris 83410*.

***Distichium inclinatum* (Hedwig) Bruch & W. P. Schimper** [Ditrichaceae]

Literature: Koch 1950a; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Showers 1982; Watson 1880.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, SN, SNE.

Selected specimens: Alpine Co.: Winnemucca Lake, Mokelumne Wilderness, Eldorado National Forest, *Norris 71260*; Fresno Co.: between Twin Lakes and Round Meadow, Kaiser Wilderness, Sierra National Forest, *Shevock & Clines 21406*; Inyo Co.: slopes above Treasure Lake west of Big Pine, John Muir Wilderness, Inyo National Forest, *Norris 46967*; Long Lake along Rock Creek Trail toward Morgan Pass, John Muir Wilderness, Inyo National Forest, *Shevock 13823*; Mono Co.: Mildred Lake, John Muir Wilderness, Inyo National Forest, *Norris 71400*; Tulare Co.: Primrose Lake, Sequoia National Park, *J.T. Howell s.n.* (CAS).

***Ditrichum ambiguum* Best** [Ditrichaceae]

Literature: Bourell 1981; Crum and Anderson 1981; Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a, 1951e; Lawton 1971; Shevock and Toren 2001; Spjut 1971; Toren 1977; Yurky 1990, 1995.

Illustrations: Crum and Anderson 1981; Lawton 1971.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Glenn Co.: about 0.5 mile north of Lone Star Camp, *Norris 47970*; Humboldt Co.: Coyote Peak on Bald Hills Road, *Norris 22341*; Lake Co.: Forest Road 18N34, about 1 mile east of The Slides west of Lake Pillsbury, Mendocino National Forest, *Toren & Bourell 5047* (CAS); Mendocino Co.: Ornbaun Creek near Mountain View Road, *Norris 53183*; Santa Cruz Co.: Ice Cream Grade, 1.6 miles west of junction with Empire Grade, *Whittemore 4439* (MO); Sonoma Co.: Gualala River near Soda Spring, *Norris 86983*; Trinity Co.: Rattlesnake Creek at Hell Gate Campground east of Forest Glen, *Norris 23817*; Tulare Co.: Clover Creek off of General's Highway, Marble Fork Kaweah River, Sequoia National Park, *Shevock 15631* (determined by Toren).

***Ditrichum heteromallum* (Hedwig) E. Britton**

[Ditrichaceae]

Literature: Jamieson 1969; Koch 1950a; Spjut 1971.

Illustrations: Ignatov and Ignatova 2003; Lawton 1971; Smith 1978.

Geographic subdivisions: CW, NW.

Selected specimens: Humboldt Co.: James Irvine Trail, Prairie Creek Redwood State Park, *Jamieson 195* (UC) and Big Lagoon, *Glade s.n.* (MO); Lake Co.: Manning Creek, Highway 175 about 4 miles west of Lakeport, *Toren 7339* (CAS); Monterey Co.: Mill Creek Picnic Area, *Norris 48568*.

***Ditrichum montanum* Leiberg** [Ditrichaceae]

Literature: Spjut 1971.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, NW.

Selected specimens: Humboldt Co.: near Round Prairie about 3 miles north of Highway 299, *Norris 52896*; Siskiyou Co.: Haypress Meadows, Marble Mountain Wilderness, Klamath National Forest, *Norris 12321*, Marble Valley Guard Station along trail to Paradise Lake, *Spjut 1185* (UC) and Doe Creek, *Norris 23064*.

***Ditrichum pusillum* (Hedwig) Hampe**

[Ditrichaceae]

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: NW, SN.

Selected specimens: Humboldt Co.: Coyote Peak on Bald Hills Road, *Norris 22351*; Placer Co.: Canyon Creek near Dutch Flat, *MacFadden 9612* (MO).

***Ditrichum schimperi* (Lesquereux) Kuntze**

[Ditrichaceae]

Literature: Holmberg 1969; Howe 1897; Kellman 2003; Koch 1950a; Lawton 1971; Shevock and Toren 2001; Smith 1970; Steere et al. 1954; Yurky 1990, 1995. As *Leptotrichum schimperi* Lesquereux 1868; Lesquereux and James 1884; Watson 1880.

Illustrations: Lawton 1971.

Geographic subdivisions: CW, NW, SN.

Selected specimens: Calaveras Co.: South Comanche shore near Burson, *Steen 840326-3* (MO); Del Norte Co.: Bear Basin Butte, *Norris 8106*; Marin Co.: Inverness Ridge above Inverness, *J.T. Howell s.n.* (CAS, UC); Lake Co.: sulfur hot springs near Anderson Springs, *Toren & Dearing 7254* (CAS); Mariposa Co.: Highway 140 at Slate Creek Bridge, *Shevock & Toren 22483*; Mendocino Co.: Pygmy Forest along County Road 409 about 1 mile east of Highway 1 south of Fort Bragg, *Norris 11722*; San Francisco Co.: Mt. Davidson, *Shevock 18926*; San Mateo Co.: Flume Trail west of Nature Center, Filoli, north of Woodside, *Whittemore 4399* (MO); Santa Cruz Co.: Sempervirens Falls, Big Basin Redwood State Park, *Koch 2063* (UC) and Henry Cowell Redwoods State Park, *Kellman 595* (UC).

***Drepanocladus aduncus* (Hedwig) Warnstorf**

[Campyliaceae]

Literature: Bourell 1981; Bradshaw 1926; Harthill et al. 1979; Ireland 1982; Janssens 1983; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Long 1978; Shevock and Toren 2001; Showers 1982; Spjut 1971; Toren 1977; Wynne 1944; Żarnowiec 2001. As *Hypnum aduncum* Brandegees 1891; Coville 1893; Lesquereux 1868; Sullivant 1856; Watson 1880.

Illustrations: Buck 1998; Flowers 1973; Hedenäs 1987, 1993a; Ireland 1982; Janssens 1983; Kanda 1978; Koponen et al. 1995; Lawton 1971; Sharp et al. 1994; Smith 1978; Żarnowiec 2001.

Geographic subdivisions: CaR, CW, MP, NW, SN, SNE, SW.

Selected specimens: Humboldt Co.: near McClellan Mountain about 5 miles east of Bridgeville, *Norris* 45814; Lake Co.: near Upper Nye Camp north of Snow Mountain Wilderness boundary, Mendocino National Forest, *Shevock, Bourell, & Toren* 15844 (CAS); Modoc Co.: Big Sage Reservoir north of Alturas, *Norris* 68476; San Bernardino Co.: Bluff Lake, San Gorgonio Wilderness, San Bernardino National Forest, *Harpel* 597 (pers. herb.); San Francisco Co.: Stonestown at 19th Avenue, San Francisco, *Toren* 8061 (CAS); Tulare Co.: Headwaters of Freeman Creek, 0.5 mile east of Quaking Aspen, Sequoia National Forest, *Shevock* 10639.

***Drepanocladus capillifolius* (Warnstorf)**
Warnstorf [Campylaceae]

Literature: Janssens 1983; Wynne 1943; Żarnowiec 2001.

Illustrations: Hedenäs 1993a; Janssens 1983; Koponen et al. 1995; Lawton 1971; Wynne 1943; Żarnowiec 2001.

Geographic subdivisions: SN, SNE.

Selected specimens: Sierra Co.: Little Truckee River, 13 miles east of Truckee, *MacFadden s.n.* (DUKE) [cited by Żarnowiec 2001] and north shore of Independence Lake, Tahoe National Forest, *Norris* 99453; Tulare Co.: Big Meadows off of Forest Road 14S11, Sequoia National Forest, *Shevock & York* 13668.

***Drepanocladus polycarpus* (Blandow ex Voit)**
Warnstorf [Campylaceae]

Literature: Żarnowiec 2001.

Illustrations: Żarnowiec 2001.

Geographic subdivisions: SN, SNE.

Selected specimens: Fresno Co.: near Marvin Pass, Jennie Lakes Wilderness, Sequoia National Forest, *Shevock & York* 13698 (determined by Ochyra); Inyo Co.: near Bishop Creek, Sabrina Basin, Inyo National Forest, *Shevock* 15294 (determined by Ochyra); Kern Co.: Kelso Creek near Rocky Point, Piute Mountains, *Shevock, Laeger, Adams, & Benson* 20268 (determined by Ochyra); Sierra Co.: Sagehen Creek, Tahoe National Forest, *Tavares & Noack* 624 (NY, UC); Tulare Co.: Oriole Lake, Sequoia National Park, *Shevock* 17618 (determined by Ochyra) and Soda Creek, Golden Trout Wilderness, Sequoia National Forest, *Laeger* 447 (determined by Ochyra).

***Drepanocladus sordidus* (C. Müller Hal.)**
Hedenäs in W. R. Buck [Campylaceae]

Literature: Misapplied as *Drepanocladus sendtneri* Hedenäs 1998; Janssens 1983. Misapplied as *Hypnum sendtneri* Howe 1896.

Illustrations: Buck 1998; Hedenäs 2003.

Geographic subdivisions: MP, SN, SNE.

Selected specimens: Modoc Co.: Big Sage Reservoir north of Alturas, *Norris* 68483; Mono Co.:

Tioga Pass Campground about 2.5 miles north of Tioga Pass, Inyo National Forest, *Norris* 48363.

***Encalypta ciliata* Hedwig** [Encalyptaceae]

Literature: Bourell 1981; Crum and Anderson 1981; Harthill et al. 1979; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Showers 1982; Spjut 1971; Toren 1977; Watson 1880.

Illustrations: Abramov and Volkova 1998; Allen 2002; Crum and Anderson 1981; Flowers 1973; Horton 1983; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Pursell and Allen 1997b; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: El Dorado Co.: Silver Creek at Rat Castle Campground, Eldorado National Forest, *Norris* 58538; Humboldt Co.: headwaters of South Fork Tish-Tang-a-Tang Creek east of Hoopa, *Norris & Whittemore* 52369 & 52405; Mariposa Co.: near Wawona Tunnel at Discovery Point, Yosemite National Park, *Shevock & Toren* 21485; Mendocino Co.: Eastman Creek about 1 mile east of Dos Rios on Highway 162, *Norris* 55008; Siskiyou Co.: Malone Creek south of Happy Camp, Klamath National Forest, *Norris* 52213; Tehama Co.: headwaters of Beegum Creek above intersection with Forest Road 35, about 1.5 miles west of Rat Trap Gap, Shasta-Trinity National Forest, *Norris* 57007 (determined by Horton); Tulare Co.: road to Mineral King about 0.5 mile east of Silver City, Sequoia National Park, *Shevock* 17656.

***Encalypta intermedia* Juratzka** [Encalyptaceae]

Illustrations: No illustration located for this species.

Geographic subdivisions: DMoj, DSon, SN, SNE.

Selected specimens: Inyo Co.: road from Big Pine to Opal Canyon, north entrance to Saline Valley, Inyo National Forest, *Norris* 79267 & 79269 and Rodgers Peak near Hummingbird Spring, Panamint Mountains, Death Valley National Park, *Shevock, York, & Davis* 21361; Kern Co.: Forest Road 27S02 along ridge, 4.2 miles above Saddle Springs, Piute Mountains, Sequoia National Forest, *Shevock* 15517 (determined by Horton); Trinity Co.: Stuart Gap Trailhead, *Norris* 56873 (determined by Horton).

***Encalypta procera* Bruch** [Encalyptaceae]

Illustrations: Crum and Anderson 1981; Horton 1983; Ignatov and Ignatova 2003; Ireland 1982; Pursell and Allen 1997b.

Geographic subdivisions: SN.

Selected specimens: Fresno Co.: Windy Gulch above Boyden Cave, Monarch Wilderness, Sequoia National Forest, *Shevock & York* 13623 (determined by Horton).

***Encalypta rhyptocarpa* Schwägrichen**
[Encalyptaceae]

Literature: Crum and Anderson 1981; Flowers 1973; Koch 1950a; Lesquereux 1868; Spjut 1971.

As *Leersia rhamnoides* Howe 1897. As *Leersia trachymitria* Coville 1893. As *Encalypta vulgaris* var. *rhamnoides* Lawton 1971.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971; Ochrya 1998a; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, MP, NW, SN, SNE.

Selected specimens: Inyo Co.: east side of Army Pass, John Muir Wilderness, Inyo National Forest, *J.T. Howell s.n.* (CAS); Modoc Co.: Big Sage Reservoir northwest of Alturas, *Norris 68498*; Mono Co.: Convict Creek above Convict Lake, Inyo National Forest, *Shevock 13795* (determined by Horton); Plumas Co.: Highway 89 about 3 miles south of Crescent Mills, Plumas National Forest, *Norris 69961* (determined by Horton); Siskiyou Co.: Beaver Creek about 4 miles north of intersection with Klamath River, *Norris 55811* (determined by Horton); Tulare Co.: Tule River near Camp Nelson, Sequoia National Forest, *Norris, Shevock, & Barahona 78683*.

***Encalypta vulgaris* Hedwig** [Encalyptaceae]

Literature: Harpel 1980a; Harthill et al. 1979; Kingman 1912; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Showers 1982; Sigal 1975; Steere et al. 1954; Toren 1977; Watson 1880. As *Encalypta vulgaris* var. *mutica* McCleary 1972; Steere 1954.

Illustrations: Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: CaR, CW, DMoj, MP, NW, SN, SNE, SW.

Selected specimens: Lake Co.: Chalk Mountain, north fork Cache Creek, *Toren & Dearing 7311* (CAS) [determined by Horton]; Los Angeles Co.: Highway 138 about 3 miles west of Palmdale, *Norris 68099* and West Fork San Gabriel River, San Gabriel Mountains, Angeles National Forest, *Harpel 2209* (pers. herb.); Mendocino Co.: Eel River about 5 miles south of Dos Rios, *Norris 67610*; Modoc Co.: Loveness Road near Highway 139 about 4 miles north of Canby, *Norris 22468*; Trinity Co.: near Coopers Bar, Shasta-Trinity National Forest, *Norris 71969*; Tulare Co.: General's Highway near Ash Mountain Headquarters, Middle Fork Kaweah River, Sequoia National Park, *Shevock & L. Norris 10168* (determined by Horton).

***Entosthodon attenuatus* (Dickson) Bryhn**

[Funariaceae]

Literature: Harthill et al. 1979; Kellman 2003; Koch 1950a; Yurky 1990, 1995. As *E. templetoni* Lesquereux 1868; Lesquereux and James 1884.

Illustrations: Allen 2002; Grout 1928–1940.

Geographic subdivisions: CW, NW.

Selected specimens: Del Norte Co.: from junction with Highway 199, 5 miles southeast on County Road 427, *Silver 898* (UC) and Smith River at

Highway 199, Jedediah Smith Redwood State Park, *Norris 68929*; Marin Co.: road to Point Reyes National Seashore, *J.T. Howell 21436* (MO, NY) [determined by Koch; Fife]; Mendocino Co.: location not specified, *Bolander s.n.* (UC); San Luis Obispo Co.: Boy Scout Road at the Palisades, Camp Roberts Military Reservation, *Norris 100926*; San Mateo Co.: near Searsville, *Bolander s.n.* (UC); Santa Cruz Co.: south side of Empire Grade at milepost 13, *Kellman 1457* (CAS) and upper U.C. Santa Cruz Campus at “four corners,” *Kellman 1461* (CAS).

***Entosthodon bolanderi* Lesquereux** [Funariaceae]

Literature: Brandegee 1891; Harthill et al. 1979; Holzinger 1892; Koch 1950a; Lesquereux 1868; Lesquereux and James 1884; McCleary 1972; Shevock and Toren 2001; Watson 1880. As *Funaria bolanderi* Bartram 1928; Sayre 1940.

Illustrations: Grout 1928–1940; Sharp et al. 1994.

Geographic subdivisions: DMoj, SN, SNE.

Selected specimens: Kern Co.: Highway 178 about 1 mile west of Walker Pass, Scodie Mountains, *Norris 87126*, Mesquite Canyon northwest of Garlock, El Paso Mountains, Mojave Desert, *Norris, Shevock and Barahona 87139*; San Diego Co.: Sea bluffs, La Jolla, *MacFadden 16872* (MO); San Francisco Co.: San Francisco, *Bolander s.n.* (NY); Trinity Co.: near Coopers Bar, Shasta-Trinity National Forest, *Norris 71979*; Tulare Co.: County Road M-99 at Limestone Campground north of Kernville, Sequoia National Forest, *Norris, Shevock, & Barahona 87101*.

***Entosthodon californicus* (Sullivan & Lesquereux) H. Crum & L. E. Anderson**
[Funariaceae]

Literature: Harthill et al. 1979; Lawton 1971; Toren 1977. As *Funaria californica* Bartram 1928; Howe 1897; Koch 1950a, 1951e; Lesquereux 1868; Lesquereux and James 1884; Watson 1880.

Illustrations: Grout 1928–1940; Lawton 1971.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Butte Co.: Big Chico Creek at northeast boundary of Bidwell Park, *Norris 70065*; Fresno Co.: Red Mountain east of Humphreys Station, *Shevock & York 13259*; Lake Co.: Manning Creek, Highway 175 about 4 miles west of Lakeport, *Toren, Bourell, Dearing, & Shevock 7001* (CAS); Mendocino Co.: Little Lake Road about 2 miles east of Mendocino, *Largent s.n.* (UC) and near Robinson Creek southwest of Ukiah, *Steere s.n.* (NY); Shasta Co.: County Road A17 at intersection of road to Black Butte, *Norris 23734 & 23744* and Highway 44 about 13 miles east of Redding, *Norris 71925*; Siskiyou Co.: about 1 mile west of Seiad Valley, *Norris 58284 & 58290*; Tulare Co.: Yucca Point Trail near Ash Mountain, Sequoia National Park, *Shevock & Whitmarsh 16994*.

****Entosthodon drummondii* Sullivant in Sullivant & Lesquereux** [Funariaceae]

Illustrations: Grout 1928–1940.

Geographic subdivisions: CaR, CW, NW.

Selected specimens: Butte Co.: south of Chico on Neal Road to Paradise about 0.5 mile east of Highway 99, *Norris* 10609; Humboldt Co.: Alliance Road at 14th Street, City of Arcata, *Norris* 67955; Monterey Co.: Sam Jones Road near Piedras Altas, Hunter-Liggett Military Reservation, *Norris* 87267; Trinity Co.: Rush Creek Road about 4 miles from Lewiston, Shasta-Trinity National Forest, *Norris* 71966.

***Entosthodon kochii* H. Crum & L. E. Anderson** [Funariaceae]

Literature: Crum and Anderson 1955.

Illustrations: Crum and Anderson 1955.

Geographic subdivisions: CW, NW, SN.

Selected specimens: Marin Co.: Lucas Valley Road about 2–3 miles east of Nicassio, *Robertson* 916 (CAS); Mariposa Co.: Highway 140 at Bear Creek Bridge along Merced River (BLM land at Briceburg), *Koch* 1733a (MICH); Mendocino Co.: U.C. Hopland Field Station, *Kellman* 2230 (CAS, MO); San Luis Obispo Co.: Nacimiento River at Twin Bridges, Camp Roberts Military Reservation, *Norris* 100950 & 100957.

****Entosthodon rubrisetus* (E. B. Bartram) Grout** [Funariaceae]

Illustrations: As *Funaria rubriseta* Bartram 1928.

Geographic subdivisions: SN, SNE.

Selected specimens: Kern Co.: Erskine Creek Canyon, 3 miles south of Lake Isabella Blvd., Piute Mountains, *Shevock & Tan* 13047 and between Erskine Creek Canyon entrance and Liebel Ranch, *Shevock* 13356; Inyo Co.: Highway 395 just south of Cinder Cone Road, *Shevock* 14789; San Bernardino Co.: Ord Mountain near Daggett, *Haring* 313 (NY).

****Entosthodon tucsoni* (E. B. Bartram) Grout** [Funariaceae]

Illustrations: As *Funaria tucsoni* Bartram 1928.

Geographic subdivisions: SN.

Selected specimens: Fresno Co.: trail to Boulder Creek from Boyden Cave, Monarch Wilderness, South Fork Kings River, Sequoia National Forest, *Shevock & York* 14513.

***Ephemerum serratum* (Schreber ex Hedwig) Hampe** [Ephemeraceae]

Literature: Brandegee 1891; Bryan and Anderson 1957; Crum and Anderson 1981; Kellman 2003; Koch 1950a; Lesquereux 1868; Shevock and Toren 2001; Toren 1977; Watson 1880. As *Ephemerum minutissimum* Crum 1957. As *Ephemerum serratum* var. *angustifolium* Lesquereux and James 1884.

Illustrations: Bryan and Anderson 1957; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Lake Co.: near Hell's Peak, *Toren* 1476 (CAS) [determined by Bryan] and Highway 53 about 1 mile south of Highway 20, *Norris* 47709; Madera Co.: near Eastman Lake, *Shevock* 14933a; San Francisco Co.: Mission Dolores, San Francisco, *Bolander s.n.* (DUKE); Santa Barbara Co.: Santa Inez Mountains about 4 miles south of Solvang, *Norris* 68160; Santa Cruz Co.: University of California, Santa Cruz, *Norris* 55679; Shasta Co.: Highway 299 about 9 miles east of Bella Vista, *Norris* 47595, 47596, & 47598; Tulare Co.: Coffee Campground off of Highway 190, Tule River Canyon, Sequoia National Forest, *Norris* 87046.

***Epipterygium tozeri* (Greville) Lindberg** [Mniaceae]

Literature: Bourell 1981; Crum 1967b; Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Shaw 1984; Shevock and Toren 2001; Smith 1970; Stark and Whittemore 1992; Steere et al. 1954; Sullivant 1856; Toren 1977; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Bryum tozeri* Lesquereux 1868; Watson 1880. As *Webera tozeri* Bradshaw 1926; Brandegee 1891; Lesquereux and James 1884.

Illustrations: Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SW.

Selected specimens: Butte Co.: Brush Creek, *Dillingham* 805 (UC); Humboldt Co.: near Round Prairie about 3 miles north of Highway 299 on Wiregrass Ridge, *Norris* 52894 (determined by Shaw); Monterey Co.: Campground at Pfeiffer-Big Sur State Park, *Norris* 75886; San Francisco Co.: Golden Gate Park, *Shevock* 18836; Santa Barbara Co.: Windmill Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock* 20886; Shasta Co.: road to Olinda about 2.3 miles east of Anderson, *Norris* 47629; Sonoma Co.: Russian Gulch about 1 mile from bridge, *Koch* 3502 (UC).

***Eucladium verticillatum* (Hedwig in Bridel) Bruch & W. P. Schimper** [Pottiaceae]

Literature: Crum and Anderson 1981; Harthill et al. 1979; Howe 1897; Kellman 2003; Kingman 1912; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Long 1978; McCleary 1972; Mishler 1978; Moxley 1928; Steere 1954; Thomson and Ketchledge 1958; Toren 1977; Yurky 1990, 1995; Zander 1977a.

Illustrations: Brotherus 1924–1925; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971; Saito 1975; Sharp et al. 1994; Smith 1978; Zander 1993.

Geographic subdivisions: CaR, CW, DMoj, DSon, GV, NW, SN, SNE, SW.

Selected specimens: Del Norte Co.: mouth of Damnation Creek, Del Norte Redwood State Park, *Norris & Taranto* 10958; Inyo Co.: Hole in the Rock Springs, Death Valley National Park, *Norris*

10201; Lake Co.: Cooper Creek near Hell's Peak, *Toren* 642 (SFSU); Riverside Co.: near Ortega Oaks Campground, Cleveland National Forest, *Norris* 58145; Santa Clara Co.: Penitencia Creek, Alum Rock Park, *Mueller & Schofield* 6922 (UC); Shasta Co.: County Road A16, 14 miles east of Platina, *Norris* 23773; Tulare Co.: Road M-99 at Limestone Campground, Kern River, Sequoia National Forest, *Shevock* 14315; Yolo Co.: Highway 16 about 2 miles northwest of Rumsey, *Norris* 70324.

***Eurhynchium hians* (Hedwig) Sande Lacoste**
[Brachytheciaceae]

Literature: Ireland 1982; Kellman 2003; Shevock and Toren 2001.

Illustrations: Ignatov 1998; Ireland 1982.

Geographic subdivisions: CW, NW, SN.

Selected specimens: Fresno Co.: Taboose Pass Trail, headwaters of South Fork Kings River, Kings Canyon National Park, *Shevock* 13860; Santa Cruz Co.: Baldwin Creek, Wilder Ranch State Park, *Kellman* 2581 (CAS); Siskiyou Co.: McKinney Creek at junction with West Fork about 6 miles south of Highway 96, Klamath National Forest, *Norris* 84914.

***Eurhynchium pulchellum* (Hedwig) Jennings**
[Brachytheciaceae]

Literature: Harthill et al. 1979; Holmberg 1969; Ireland 1982; Koch 1950a; McCleary 1972; McGrew 1976; Showers 1982; Spjut 1971; Steere 1954; Yurky 1990, 1995. As *Eurhynchium diversifolium* Wynne 1943. As *Eurhynchium strigosum* Bradshaw 1926; Lesquereux 1868; Sayre 1940. As *Eurhynchium strigosum* var. *scabrisetum* Sayre 1940. As *Eurhynchium substrigosum* Flowers 1973; Koch 1950a, 1951e, 1958; Lawton 1971; Spjut 1971. As *Hypnum strigosum* Howe 1897; Watson 1880.

Illustrations: Abramov and Volkova 1998; Buck 1998; Flowers 1973; Ireland 1982; Lawton 1971; Smith 1978; Ignatov 1998.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Alpine Co.: Highway 4 at Stanislaus Meadows Trailhead, Stanislaus National Forest, *Norris* 78997; Del Norte Co.: Doctor Rock, Six Rivers National Forest, *Norris* 50284; Fresno Co.: Redwood Creek, Windy Gulch Redwood Grove, Sequoia National Forest, *Norris*, *Shevock*, & *York* 87940; Plumas Co.: Onion Valley Creek near Pacific Crest Trail, Plumas National Forest, *Norris* 83184; Siskiyou Co.: South Fork Lakes west of Callahan, Klamath National Forest, *Norris* 76902; Tulare Co.: Clover Creek, Marble Fork Kaweah River, Sequoia National Park, *Shevock* 15633; Tuolumne Co.: Porcupine Creek Trail near Tuolumne Meadows, Yosemite National Park, *Norris* 100380.

****Eurhynchium striatum* (Schreber ex Hedwig) W. P. Schimper** [Brachytheciaceae]

Illustrations: Smith 1978.

Geographic subdivisions: CaR, SN.

Selected specimens: Plumas Co.: Forest Road 22N94, un-named tributary to South Fork Middle Fork Feather River, Plumas National Forest, *Dillingham* 747 (CAS), Dixie Canyon about 0.5 mile from Highway 89, *Shevock*, *Ertter*, & *Moroso* 15736, just south of Turkeytown, 1 air mile east of Blue Nose Mountain and 10 miles northeast of LaPorte, Plumas National Forest, *Ahart* 10501 (UC), Domingo Spring, 8 miles northwest of Chester, Lassen National Forest, *Dillingham* 965 (CAS).

***Fabronia ciliaris* (Bridel) Bridel** [Fabroniaceae]

Literature: As *Fabronia octoblepharis* Kingman 1912.

Illustrations: Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: CW, NW, SN, SW.

Selected specimens: Lake Co.: Highway 53 about 1 mile south of Highway 20, *Norris* 47677; Los Angeles Co.: La Tuna Canyon, Verdugo Hills, *MacFadden* 8097 (MO) [determined by Grout]; Monterey Co.: Sam Jones Road about 1 km east of Piojo Airstrip, Hunter-Liggett Military Reservation, *Norris* 87260; Nevada Co.: Slacks Ravine along Highway 20 about 7 miles west of Rough and Ready, *Norris* 67484; Shasta Co.: County Road A17 at intersection with Black Butte Road, *Norris* 23747, Interstate 5 about 3 miles north of the Tehama County line, *Norris* 48217 and Shasta College turnoff north of Redding, *Norris* 57766; Sutter Co.: Philip Road near junction with Fiddymont Road northwest of Roseville, *Norris* 103669.

***Fabronia pusilla* Raddi** [Fabroniaceae]

Literature: Bradshaw 1926; Harthill et al. 1979; Howe 1896; Kellman 2003; Koch 1950a, 1951e; Lawton 1971; Lesquereux 1868; Long 1978; Mishler 1978; Thomson and Ketchledge 1958; Toren 1977; Watson 1880.

Illustrations: Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: CaR, CW, DMOj, NW, SN, SW.

Selected specimens: Contra Costa Co.: Mount Diablo State Park about 1.5 miles from entrance, *Koch* 1552 (UC); Inyo Co.: South Fork Hanaupah Canyon, east base of Telescope Peak, Death Valley National Park, *Shevock* & *York* 21354; Kern Co.: Horse Canyon, tributary of Cache Creek, 4 miles north of Highway 58, southern Piute Mountains, *Shevock* & *Hare* 14900; San Bernardino Co.: Waterman Canyon, San Bernardino National Forest, *Harpel* 2400 (pers. herb.); Tehama Co.: Antelope Creek Canyon near Microwave Station about 10 miles east of Red Bluff, *Berti* 415 (UC); Trinity Co.: Hall City Caves east of Wildwood, Shasta-Trinity National Forest, *Norris* 71664; Ventura Co.: Howard Creek Trail about 1 mile east of Highway

399, *Norris* 55483; Yuba Co.: Highway 20 near Timbuctoo, *Norris* 67488.

***Fissidens adianthoides* Hedwig** [Fissidentaceae]

Literature: Barnes 1887; Frantz and Cordone 1967; Grout 1928–1940; Koch 1950a.

Illustrations: Ignatov and Ignatova 2003; Smith 1978.

Geographic subdivisions: SN.

Selected specimens: Placer Co.: off of Chambers Point submerged at a depth of 244 feet in Lake Tahoe with *Fissidens bryoides* and *F. grandifrons*, Lake Tahoe Basin Management Unit, *Frantz s.n.* (WTU) [determined by Lawton; confirmed by Pursell].

***Fissidens aphelotaxifolius* Pursell**

[Fissidentaceae]

Literature: McGrew 1976; Pursell 1976a.

Illustrations: Pursell 1976a.

Geographic subdivisions: NW, SN.

Selected specimens: Madera Co.: tributary of Owl Creek 0.75 mile east of Whisky Falls, Sierra National Forest, *Shevock, Norris, Beyer, & Price* 20225 (confirmed by Pursell); Siskiyou Co.: Lower Russian Lake overflow, Klamath National Forest, *McGrew* 322 (HSC) [determined by Pursell].

Fissidens bryoides* Hedwig var. *bryoides

[Fissidentaceae]

Literature: Barnes 1887; Bourell 1981; Bradshaw 1926; Crum and Anderson 1981; Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Moxley 1928; Showers 1982; Smith 1970; Spjut 1971; Yurky 1990.

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Iwatsuki and Suzuki 1982; Lawton 1971; Smith 1978.

Notes: Pursell recognizes two varieties under *Fissidens bryoides* for California. We cite below collections determined by Pursell as representing these varieties.

Geographic subdivisions: SN, SNE, SW.

Selected specimens: Fresno Co.: below Fifth Baxter Lake, Kings Canyon National Park, *Shevock & York* 16588 (determined by Pursell); Inyo Co.: Whitney Portal Road, 2.2 miles west of Lone Pine, Lone Pine Creek, Alabama Hills, *Shevock & Norris* 16855 & 16859 (determined by Pursell); Placer Co.: Dutch Flat, *MacFadden* 16863 (MO) [determined by Pursell] and off of Chambers Point submerged at a depth of 244 feet in Lake Tahoe, Lake Tahoe Basin Management Unit, *Frantz s.n.* (WTU) [determined by Pursell]; San Diego Co.: Matagual Creek, Volcan Mountains, *Stark* 602 & 603 (MO) [determined by Pursell]; Tulare Co.: General's Highway, 2.1 miles above Potwisha Campground, Middle Fork Kaweah River, Sequoia National Park, *Shevock* 15181 and North Fork Kern River above Forks of the Kern, Golden Trout Wilderness, Se-

quoia National Forest, *Shevock* 16525 (determined by Pursell).

****Fissidens bryoides* Hedwig var. *pusillus***

(Wilson) Pursell [Fissidentaceae]

Illustrations: Crum and Anderson 1981; Pursell 1976b; Pursell and Allen 1996a; Sharp et al. 1994.

Geographic subdivisions: NW.

Selected specimens: Mendocino Co.: North Coast Range Preserve, about 7 miles north of Branscomb, *Bourell* 1391 (CAS, MO) [determined by Pursell].

Fissidens bryoides* Hedwig var. *viridulus

(Swartz) Brotherus [Fissidentaceae]

Literature: As *Fissidens bryoides* var. *longifolius* Shevock and Toren 2001.

Illustrations: Crum and Anderson 1981.

Geographic subdivisions: CW, NW, SN.

Selected specimens: Lake Co.: Sweetwater Creek, Hidden Valley, *Toren & Dearing* 7075 (CAS) [determined by Pursell]; Placer Co.: Forest Hill, road to Colfax, *MacFadden* 16962 (MO) [determined by Pursell]; San Francisco Co.: Golden Gate Park, *Hermann* 17449 (CAS) [determined by Pursell]; Tuolumne Co.: Vernal Falls, Yosemite National Park, *Ikenberry* 1358a (MO) [determined by Pursell].

***Fissidens crispus* Montagne** [Fissidentaceae]

Literature: Kellman 2003; Pursell 1997b; Shevock and Toren 2001. As *Fissidens limbatus* Brandegee 1891; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Kingman 1912; Koch 1949a, 1950a; Koch and Ikenberry 1954; Lesquereux 1868; Lesquereux and James 1884; Long 1978; McCleary 1972; Millspaugh and Nuttall 1923; Mishler 1978; Moxley 1928, 1931; Sayre 1940; Sigal 1975; Steere 1954; Sullivant 1856; Toren 1977; Watson 1880; Whittemore and Sommers 1999; Yurky 1995.

Illustrations: Flowers 1973; Sharp et al. 1994.

Geographic subdivisions: CaR, CW, GV, NW, SN, SW.

Selected specimens: Colusa Co.: about 1.2 miles east of Sites, *Norris* 72681; Fresno Co.: Cripe Road, 0.65 mile from Peterson Mill Road, Sierra National Forest, *Shevock & York* 14949 (confirmed by Pursell); Kern Co.: Bodfish-Havilah Road, 0.5 mile south of Bodfish Gap, base of Piute Mountains, *Shevock & Tan* 13041 (determined by Pursell); Lake Co.: Highway 53 about 1 mile south of Highway 20, *Norris* 47703; San Francisco Co.: Mt. Sutro, *Shevock* 19175 (determined by Pursell); Santa Barbara Co.: Lobos Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock & Rodriguez* 20855 (determined by Pursell); Tehama Co.: end of Buckhorn Road, BLM Black Butte Recreation Area, *Norris & Piippo* 82376; Tulare Co.: about 0.5 mile above Buckeye Campground, trailhead for Middle Fork Kaweah River Trail, Sequoia National Park, *Shevock* 15212 (determined by Pursell).

***Fissidens curvatus* Hornschuch** [Fissidentaceae]

Literature: Kellman 2003; Shevock and Toren; Whittemore and Sommers 1999. As *Fissidens milobakeri* Koch 1951c; Pursell 1979; Yurky 1990, 1995.

Illustrations: Sharp et al. 1994.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Alameda Co.: UC Berkeley Campus, Strawberry Canyon about 0.5 mile above the Botanic Garden, *Norris* 82603; Butte Co.: Big Chico Creek about 3 miles southwest of upper boundary of Bidwell Park, *Norris* 70092; Nevada Co.: Slack's Ravine along Highway 20 about 7 miles west of Rough and Ready, *Norris* 67468; San Francisco Co.: Coastal Bluff Trail, Golden Gate National Recreation Area, *Shevock* 18886; San Luis Obispo Co.: Santa Rosa Creek about 0.5 mile east of Cambria, *Norris* 68216; Santa Clara Co.: Stanford Campus, *Wiggins* 22715 (MO) [determined by Pursell]; Shasta Co.: Highway 299 about 1 mile east of Shingletown, *Norris* 52846.

****Fissidens dubius* Palisot de Beauvois**

[Fissidentaceae]

Illustrations: Ignatov and Ignatova 2003. As *Fissidens cristatus* Crum and Anderson 1981.

Geographic subdivisions: CW.

Selected specimens: San Francisco Co.: Japanese Tea Garden, Golden Gate Park, *Toren* 8951 (CAS, PAC) [determined by Pursell].

***Fissidens fontanus* (Bachelot de la Pylaie)**

Steudel [Fissidentaceae]

Literature: Crum and Anderson 1981; Kellman 2003; Lawton 1971; Toren 1977; Yurky 1990, 1995. As *Octodiceras fontanum* Koch 1950a. As *Octodiceras julianum* Britton 1902.

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Koponen et al. 1995; Lawton 1971; Pursell 1987; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CW, NW, SN.

Selected specimens: Kern Co.: Kern River along Highway 178 near Richbar, Sequoia National Forest, *Shevock* 12883 & 16763 (confirmed by Pursell) and outlet of Lake Isabella, *Laeger* 528 (CAS, PAC, UC); Lake Co.: south shore Clear Lake at Corinthian Bay County Park, *Norris* 71780, City of Clear Lake Public Pier, *Toren* 6845 (CAS), Clear Lake State Park, *Toren* 6846 (CAS) east shore of Blue Lakes, *Toren* 523 (SFSU) and Rodman Slough near Upper Lake, *Shevock & Toren* 20306; Marin Co.: Lily Lake, *Toren* 963 (SFSU); Napa Co.: Weeks Ranch about 3 miles from Calistoga towards Petrified Forest, *Koch* 1397 (UC); Santa Cruz Co.: Quail Hollow Pond, Quail Hollow Ranch County Park, *Kellman* 2613 (CAS).

***Fissidens grandifrons* Bridel** [Fissidentaceae]

Literature: Barnes 1887; Bourell 1981; Crum and Anderson 1981; Flowers 1973; Frantz and Cordone 1967; Harthill et al. 1979; Holmberg 1969; Howe

1896; Kellman 2003; Kingman 1912; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Long 1978; Mishler 1978; Spjut 1971; Watson 1880; Yurky 1990, 1995.

Illustrations: Crum and Anderson 1981; Flowers 1973; Iwatsuki and Suzuki 1982; Lawton 1971; Pursell and Allen 1994.

Geographic subdivisions: CaR, CW, NW, SN, SW.

Selected specimens: Humboldt Co.: Shelter Cove, BLM Kings Range National Recreation Area, *Norris & Piippo* 82478; Los Angeles Co.: San Antonio Creek, Mt. Baldy Camp, Angeles National Forest, *MacFadden* 17156 (MO); Marin Co.: slopes of Mt. Tamalpais, *Koch* 2262 (UC); Monterey Co.: Big Sur River, Big Sur Redwood State Park, *Koch* 3643 (UC); Placer Co.: road to Bowman Lake about 2 miles north of Highway 20, *Norris* 77001; Plumas Co.: Highway 24 along North Fork Feather River, Plumas National Forest, *Koch* 1893 (UC); Siskiyou Co.: about 1.2 miles north of Cook and Green Pass, Rogue River National Forest, *Shevock & Toren* 20115; Tulare Co.: Dark Canyon along road to Jack Ranch near White River Campground, Sequoia National Forest, *Shevock* 14294 (confirmed by Pursell).

***Fissidens minutulus* Sullivant** [Fissidentaceae]

Literature: Shevock and Toren 2001. As *Fissidens incurvus* var. *minutulus* Barnes 1887.

Illustrations: Sullivant 1864.

Geographic subdivisions: CW.

Selected specimens: San Francisco Co.: Golden Gate Park, De Laveaga Dell, AIDS Memorial Grove, *Shevock* 20284 (determined by Pursell).

***Fissidens pauperculus* M. A. Howe**

[Fissidentaceae]

Literature: Holmberg 1969; Howe 1894; Jamieson 1969; Kellman 2003; Koch 1948, 1949a, 1950a, 1951d; Lawton 1971; Steere et al. 1954; Yurky 1990, 1995.

Illustrations: Howe 1894; Lawton 1971.

Geographic subdivisions: CaR, CW, NW.

Selected specimens: Butte Co.: near Watson Ridge, *Dillingham* 779 (CAS) and tributary to Ponderosa Reservoir, 1.5 miles northwest of Fobestown, *Dillingham* 929 (CAS); Del Norte Co.: Stout Memorial Grove, *Koch* 3811 (UC); Humboldt Co.: James Irvine Trail, Prairie Creek Redwoods State Park, *Jamieson* 173 (UC), Arcata City Forest about 1 mile from Fickle Hill Road, *Norris* 68754 and Jolly Giant Creek about 0.5 mile east of Humboldt State University, *Norris* 85082a; Marin Co.: Mill Valley, *Howe s.n.* (UC) and Dipsea Trail, Mt. Tamalpais State Park, *Yurky* 785 (SFSU); Mendocino Co.: Montgomery Creek Redwoods State Park, *Kellman* 2188 (CAS); Santa Cruz Co.: along Loma Prieta Grade Trail, Forest of Nisene Marks State Park, *Kellman* 2637 (CAS).

***Fissidens sublimbatus* Grout** [Fissidentaceae]

Literature: Kellman 2003; Pursell 1997a; Shevock and Toren 2001.

Illustrations: Pursell 1997a; Sharp et al. 1994.

Geographic subdivisions: CaR, CW, DMoj, DSon, MP, NW, SN, SNE, SW.

Selected specimens: Kern Co.: Short Canyon Trail west of L.A. Aqueduct, Owens Peak BLM Wilderness, *Shevock & Newberry 16979* (determined by Pursell); Lake Co.: Hidden Valley north of Middletown, *Toren & Dearing 7373a* (CAS) [determined by Pursell]; Lassen Co.: Johnsondale Dump Road southeast of Susanville, *Norris 52838*; Los Angeles Co.: La Tuna Canyon, Verdugo Hills, *MacFadden 8085* (MO) [determined by Pursell]; San Bernardino Co.: Keystone Canyon, New York Mountains, Mojave National Preserve, *Laeger & Davis 1328* (CAS, PAC) [determined by Pursell]; San Diego Co.: Highway 94, 2 miles west of Tecate Road, *Stark 813* (MO) [determined by Pursell]; San Francisco Co.: Coastal Bluff Trail, Presidio of San Francisco, *Shevock 18945* (determined by Pursell); Santa Barbara Co.: Water Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock & Rodriguez 20832*; Shasta Co.: Highway 299 about 9 miles east of Bella Vista, *Norris 47616*.

****Fissidens taxifolius* Hedwig** [Fissidentaceae]

Illustrations: Smith 1978.

Geographic subdivisions: CW.

Selected specimens: Contra Costa Co.: Jewel Lake Trail, Tilden Regional County Park, *Norris & Hill-yard 105188* (confirmed by Pursell).

***Fissidens taylorii* C. Müller Hal.** [Fissidentaceae]

Literature: Kellman 2003.

Illustrations: Pursell 1997c. As *F. geheebii* Sharp et al. 1994.

Geographic subdivisions: CW.

Selected specimens: Santa Cruz Co.: Headwaters of Old Dairy Gulch near Wilder Ridge Loop Trail, Wilder Ranch State Park, *Kellman 2252* (CAS) [determined by Pursell].

***Fissidens ventricosus* Lesquereux** [Fissidentaceae]

Literature: Bourell 1981; Holmberg 1969; Ireland and Schofield 1967; Kellman 2003; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Toren 1977; Watson 1880. As *F. rufulus* Barnes 1887; Conard 1951; Koch 1950a, 1951e; Koch and Ikenberry 1954; Thomson and Ketchledge 1958.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Alameda Co.: Codornices Park, *S.F. Cook 16* (UC); El Dorado Co.: Highway 50, South Fork American River at Bridal Veil Falls Campground, Eldorado National Forest, *Norris 58407*; Fresno Co.: South Fork Kings River along Highway 180 near Grizzly Falls, Sequoia National Forest, *Shevock & York 14507* (confirmed by Pur-

sell); Humboldt Co.: Ten Taypo Trail, Prairie Creek Redwood State Park, *Norris 56820*; Kern Co.: Highway 178 just west of Richbar Picnic Area, Sequoia National Forest, *Shevock 12882* (confirmed by Pursell); Lake Co.: Gunning Creek, south slopes of Cobb Mountain, *Toren & Dearing 7119* (CAS); Mariposa Co.: Bishop Creek near confluence with South Fork Merced River, Sierra National Forest, *Shevock & Fritzke 21521*; Santa Cruz Co.: Opal Creek, Big Basin Redwoods State Park, *Kellman 1011* (CAS); Sonoma Co.: Pocket Canyon west of Forestville, *Norris 53169*.

***Fontinalis antipyretica* Hedwig** [Fontinalaceae]

Literature: Bourell 1981; Harpel 1980a; Harthill et al. 1979; Koch 1950a, 1958; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Long 1978; McGrew 1976; Showers 1982; Spjut 1971; Toren 1977; Watson 1880; Welch 1960. As *Fontinalis antipyretica* var. *patula* Lawton 1971. As *Fontinalis californica* Sullivant 1864. As *Fontinalis patula* Koch 1950a; Welch 1960.

Illustrations: Brotherus 1924–1925; Flowers 1973; Ireland 1982; Koponen et al. 1995; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, CW, MP, NW, SN, SW.

Selected specimens: Colusa Co.: Summit Springs south of Snow Mountain, Mendocino National Forest, *Norris 76101*; Marin Co.: Mt. Tamalpais, *Eastwood s.n.* (UC); Modoc Co.: Hulbert Creek north of Cottonwood Flat Campground, Modoc National Forest, *Norris 77925*; Riverside Co.: San Jacinto Mountains, San Bernardino National Forest, *Parish 1684* (UC); Siskiyou Co.: Echo Lake north of Red Butte about 5 air miles north of Seiad Valley, *Norris 57589*; Tulare Co.: Freeman Creek near Pyles Camp, Lloyd Meadows Basin, Sequoia National Forest, *Shevock 4327*.

***Fontinalis chrysophylla* Cardot** [Fontinalaceae]

Literature: As *Fontinalis antipyretica* var. *oregonensis* Lawton 1971.

Illustrations: Lawton 1971; Welch 1960.

Geographic subdivisions: NW, SN.

Selected specimens: Del Norte Co.: Hardscrabble Creek at Smith River west of Gasquet, Six Rivers National Forest, *Norris 10877*; Lake Co.: Upper Nye Camp near Snow Mountain Wilderness Trailhead, Mendocino National Forest, *Toren, Bourell, & Shevock 5167* (CAS) [determined by Allen]; Mariposa Co.: Glacier Point Road about 1.2 miles east of Bridalveil Campground, Yosemite National Park, *Norris & Shevock 100322*; Tuolumne Co.: Middle Fork Tuolumne River at Middle Fork Campground, Stanislaus National Forest, *Norris & Shevock 103986*.

***Fontinalis gigantea* Sullivant** [Fontinalaceae]

Literature: As *Fontinalis antipyretica* var. *gigantea* Watson 1880.

Illustrations: Ireland 1982; Welch 1960.

Geographic subdivisions: MP, NW, SN.
Selected specimens: Del Norte Co.: Sanger Lake southeast of O'Brien, *Norris* 70805; Fresno Co.: Redwood Creek, Windy Gulch Redwood Grove, Sequoia National Forest, *Norris, Shevock, & Barahona* 87991; Lake Co.: tributary to Stony Creek near Crockett Peak, boundary of Snow Mountain Wilderness, Mendocino National Forest, *Shevock* 15821 (determined by Allen); Modoc Co.: Yellow-jacket Springs, Modoc National Forest, *Norris* 68511; Tulare Co.: outlet of Oriole Lake, Sequoia National Park, *Shevock, Norris, & Barahona* 13170; Tuolumne Co.: Mill Creek below Cascade Creek Campground, Stanislaus National Forest, *Norris* 78801.

***Fontinalis howellii* Renauld & Cardot**
[Fontinalaceae]

Literature: Koch 1950a; Spjut 1971; Toren 1977.
Illustrations: Lawton 1971; Welch 1960.
Geographic subdivisions: CaR, NW, SN, SNE.
Selected specimens: Alpine Co.: Red Lake Creek, Toiyabe National Forest, *Norris* 88134; Fresno Co.: Cedar Grove just below Zumwalt Meadows along South Fork Kings River, Kings Canyon National Park, *Shevock* 13739; Inyo Co.: Mulkey Meadow near Whitney Portal west of Lone Pine, Inyo National Forest, *Norris* 75598; Lake Co.: Tule Lake, Mt. Sanhedrin, Mendocino National Forest, *Toren* 5116 (CAS); Trinity Co.: Bee Creek along Onion Lake Road about 7 miles south of Onion Lake, *Norris & Rivera* 72548; Tuolumne Co.: Hull Creek Campground about 14 miles east of Long Barn, Stanislaus National Forest, *Norris* 78748.

***Fontinalis hypnoides* C. J. Hartman**
[Fontinalaceae]

Literature: McGrew 1976. As *Fontinalis hypnoides* var. *duriaei* Lawton 1971; Toren 1977. As *Fontinalis duriaei* Koch 1950a. As *Fontinalis niti-da* Frantz and Cordone 1967; Welch 1960.
Illustrations: Flowers 1973; Ireland 1982; Koponen et al. 1995; Lawton 1971; Welch 1960.
Geographic subdivisions: CaR, NW, SN, SNE.
Selected specimens: Alpine Co.: Grass Lake west of Luther Pass, Eldorado National Forest, *Norris* 71321; El Dorado Co.: Ropi Lake, Desolation Wilderness, Eldorado National Forest, *Norris* 71110; Lake Co.: Blue Slides Lake south of Snow Mountain Wilderness, Mendocino National Forest, *Toren* 5261 (CAS) [determined by Allen]; Nevada Co.: about 0.5 mile northeast of Bowman Lake, Tahoe National Forest, *Ahart* 10611 (UC); Plumas Co.: headwaters of Feather River, *Austin s.n.* (UC); Mono Co.: near Barney Lake, Toiyabe National Forest, *Norris* 67170; Shasta Co.: Highway 299 about 1 mile west of Montgomery Creek, *Norris* 68597; Siskiyou Co.: Taylor Lake, Klamath National Forest, *Norris* 83432; Tulare Co.: Big Meadows off of Forest Road 14S11, Sequoia National Forest, *Shevock & York* 13664.

***Fontinalis mollis* C. Müller Hal.** [Fontinalaceae]
Literature: As *Fontinalis antipyretica* var. *mollis* Welch 1960.
Illustrations: Flowers 1973; Lawton 1971.
Geographic subdivisions: NW, SN.
Selected specimens: Lake Co.: Copsey Creek about 1 mile east of Lower Lake, *Toren* 7330 (CAS) [determined by Allen]. Tulare Co.: Long Meadow Creek at Forest Road 22S82, Sequoia National Forest, *Kellman* 1466 (CAS).

***Fontinalis neomexicana* Sullivant & Lesquereux**
[Fontinalaceae]
Literature: Howe 1896; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; McGrew 1976; Showers 1982; Spjut 1971; Watson 1880; Welch 1960. As *Fontinalis mercediana* Lesquereux 1868.
Illustrations: Lawton 1971; Sharp et al. 1994; Welch 1960.

Geographic subdivisions: CaR, CW, NW, SN, SNE.
Selected specimens: Del Norte Co.: Smith River in Jedediah Smith State Park, *Norris* 67356; Fresno Co.: Ten Mile Creek at Ten Mile Campground, Sequoia National Forest, *Shevock & York* 13691; Lake Co.: Bucknell Creek north of Horse Mountain, Mendocino National Forest, *Toren* 7452 (CAS) [determined by Allen]; Mariposa Co.: Bridalveil Creek along Glacier Point Road, Yosemite National Park, *Shevock & Norris* 20190; Mono Co.: Highway 108 west of Bridgeport at Leavitt Station Campground, *Norris* 77041; Placer Co.: Spruce Creek, *Koch* 3211 (UC); Santa Cruz Co.: Semper-virens Creek, Big Basin Redwoods State Park, *Koch* 2071 (MICH); Siskiyou Co.: Shackleford Creek, Marble Mountains, Klamath National Forest, *Spjut* 756 (UC).

****Funaria calvescens* Schwägrichen** [Funariaceae]
Illustrations: Allen 2002.
Geographic subdivisions: CaR, CW, DMoj, SN, SW.
Selected specimens: Butte Co.: Honey Run Road, 4 miles east of Covered Bridge about 12 miles east of Chico, *Taylor* 7 (UC); Fresno Co.: Coalinga-Mineral Springs State Park west of Coalinga, *Norris* 68064; Inyo Co.: Emigrant Springs, Death Valley National Park, *Shevock & Harpel* 19048; Kern Co.: South Rim Road, town of Bodfish, *Laeger* 737 (CAS, UC).

***Funaria hygrometrica* Hedwig** [Funariaceae]
Literature: Bourell 1981; Bradshaw 1926; Coville 1893; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Kellman 2003; Kingman 1912; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Long 1978; McCleary 1972; Millspaugh and Nuttall 1923; Mishler 1978; Moxley 1928; Sayre 1940; Shevock and Toren 2001; Showers 1982; Sigal 1975; Spjut

1971; Steere 1954; Steere et al. 1954; Strid 1974; Sullivant 1856; Toren 1977; Watson 1880; Whittmore and Sommers 1999; Yurky 1990, 1995. As *Funaria convoluta* Bartram 1928; Howe 1896; Kingman 1912; Lesquereux 1868; Lesquereux and James 1884; Watson 1880. As *Funaria hibernica* Lesquereux 1868. As *Funaria hygrometrica* var. *convoluta* Cooke 1941.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, DMoj, DSon, GV, MP, NW, SN, SNE, SW.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris* 87166; Fresno Co.: Ross Landing Road at Indian Head, Sierra National Forest, *Shevock, Ertter, & York* 13484; Humboldt Co.: Eyesee Road at China Gulch, Six Rivers National Forest, *Norris* 22150; Los Angeles Co.: Wrigley Memorial Gardens, Santa Catalina Island, *Harpel* 2402 (pers. herb.); Merced Co.: future campus site of University of California, Merced, *Norris* 103117; Modoc Co.: north of Middle Alkali Lake northeast of Cedarville, *Norris* 47478; Santa Barbara Co.: Lobos Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock & Rodriguez* 20845; Solano Co.: Jepson Prairie Preserve east of Fairfield, *Norris* 101393.

***Funaria microstoma* Bruch ex W. P. Schimper** [Funariaceae]

Literature: Fife 1979; Koch 1950a; Lesquereux 1868; Lesquereux and James 1884; Watson 1880.

Illustrations: Fife 1979.

Geographic subdivisions: CW, DMoj, DSon, GV, SN, SNE.

Selected specimens: Kern Co.: Erskine Creek Canyon, 3 miles south of Lake Isabella Blvd., Piute Mountains, *Shevock & Tan* 13048; Fresno Co.: Redwood Creek above Highway 180, Monarch Wilderness, Sequoia National Forest, *Shevock & York* 12692; Monterey Co.: Pinnacles, Hunter-Liggett Military Reservation, *Norris* 87289 and Sulfur Creek Road near junction with Milpitas Road, Hunter-Liggett, *Norris* 87365; San Diego Co.: Borrego Palm Canyon, Anza Borrego State Park, Colorado Desert, *Norris* 50577; Sierra Co.: Little Truckee River, 13 miles from Hobart Mill, *MacFadden* 21385 (MO); Tehama Co.: Antelope Creek Canyon about 10 miles east of Red Bluff along Bell Mill Road, *Berti* 412 (UC).

***Funaria muhlenbergii* Turner** [Funariaceae]

Literature: Christy and Wagner 1996; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Howe 1896; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; McCleary 1972; Mishler 1978; Sayre 1940; Shevock and Toren 2001; Steere 1954; Toren 1977; Whittmore and Sommers 1999. As *Funaria calcaria* Kingman 1912; Watson 1880. As *Funaria hibernica* Sullivant 1856. As *Funaria mediterranea*

Bartram 1928; Brandege 1891; Millspaugh and Nuttall 1923; Moxley 1928. As *Entosthodon muhlenbergii* Crosby et al. (2000).

Illustrations: Flowers 1973; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CW, GV, NW, SN, SW. **Selected specimens:** El Dorado Co.: Salmon Falls Road about 5 miles south of Pedro Hill Road, *Whittmore* 4344 (MO); Humboldt Co.: Highway 96 at Norton Creek, *Norris* 56662; Inyo Co.: Johnson Canyon, Panamint Mountains, Death Valley National Park, *Shevock, Harpel, & York* 19068; Los Angeles Co.: between Black Jack Campground and Mt. Orizaba, Santa Catalina Island, *Shevock & Thorne* 4037; Sacramento Co.: Mormon Island, *Copeland* 1409 (UC); Santa Cruz Co.: Blue Cliff, Henry Cowell Redwoods State Park, *Kellman* 663 (CAS); Stanislaus Co.: about 2 miles east of Oakdale, *Koch* 1474 (UC); Tulare Co.: PG&E access road crossing the Wishon Fork Tule River, Sequoia National Forest, *Shevock* 10336.

***Grimmia alpestris* (Weber & D. Mohr) Schleicher** [Grimmiaceae]

Literature: Cooke 1941; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Muñoz 1997, 1998b; Spjut 1971; Steere et al. 1954.

Illustrations: Flowers 1973; Greven 2003; Ignatov and Cao 1994; Ignatov and Ignatova 2003; Lawton 1971; Muñoz 1998b; Smith 1978.

Geographic subdivisions: SN.

Selected specimens: Fresno Co.: Highway 168 northeast of Shaver Lake, Sierra National Forest, *Norris* 99921; Nevada Co.: Donner Pass Rest Area, Highway 80, Tahoe National Forest, *Whittmore* 3031 (MO) [determined by Muñoz]; Tulare Co.: Kern Plateau near Blackrock Station, Sequoia National Forest, *Shevock* 18411 (determined by Muñoz) and Rock Creek north of Rock Creek Lake, Sequoia National Park, *Shevock* 18567 (determined by Muñoz).

***Grimmia anodon* Bruch & W. P. Schimper** [Grimmiaceae]

Literature: Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Ireland and Miller 1982; Koch 1950a, 1958; Lawton 1971; Lesquereux and James 1884; Long 1978; Showers 1982; Strid 1974. As *Grimmia apocarpa* var. *pulvinata* Showers 1982.

Illustrations: Crum and Anderson 1981; Flowers 1973; Greven 2003; Ignatov and Cao 1994; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Muñoz 1999a; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: DMoj, DSon, MP, NW, SN, SNE.

Selected specimens: Inyo Co.: Aguerberry Point, Death Valley National Park, *Shevock & Harpel* 19053 (determined by Muñoz) and Taboose Pass Trail, John Muir Wilderness, Inyo National Forest, *Shevock* 13874 (determined by Muñoz); Kern Co.: canyon between Middle Knob and Barren Ridge,

Hare 203 (CAS) [determined by Muñoz]; Lake Co.: Hull Mountain Summit, Mendocino National Forest, *Toren* 7176a (CAS) and West Peak, Snow Mountain Wilderness, Mendocino National Forest, *Toren & Dearing* 7472 (CAS); San Bernardino Co.: north side of Peak 3607, Mojave Desert, *Laeger* 873 (CAS) [determined by Muñoz].

***Grimmia anomala* Hampe in W. P. Schimper** [Grimmiaceae]

Literature: Misapplied as *Grimmia hartmannii* Harpel 1980a; Harthill et al. 1979; Koch 1950a; Lawton 1971; Long 1978; Mishler 1978; Showers 1982; Spjut 1971.

Illustrations: Greven 2003; Ignatov and Ignatova 2003. As *Grimmia hartmannii* var. *anomala* Crum and Anderson 1981; Flowers 1973.

Geographic subdivisions: CaR, NW.

Selected specimens: Del Norte Co.: Doctor Rock, *Norris* 57676 (determined by Muñoz); El Dorado Co.: Ropi Lake, *Norris* 71109 (determined by Muñoz); Humboldt Co.: Big Hill Road at South Fork Mill Creek, Six Rivers National Forest, *Norris* 58636; Plumas Co.: Quincy-La Porte Road at Onion Valley, Plumas National Forest, *Norris* 83187; Tehama Co.: Doll Basin Research Natural Area, Mendocino National Forest, *Toren & Bourell* 6666 (CAS).

***Grimmia arcuatifolia* Kindberg** [Grimmiaceae]

Literature: Muñoz 1999b.

Illustrations: Muñoz 1999b.

Notes: This species is not recognized by Greven (2003).

Geographic subdivisions: NW.

Selected specimens: Humboldt Co.: Bear Butte, *Branscomb & Greenman* 22826 (MO) [determined by Muñoz].

***Grimmia caespiticia* (Bridel) Juratzka** [Grimmiaceae]

Literature: Muñoz 1998b. As *G. alpestris* var. *manniae* Grout 1928–1940.

Illustrations: Greven 2003; Muñoz 1998b.

Geographic subdivisions: NW, SN, SNE.

Selected specimens: Inyo Co.: Big Pine Creek and Mt. Whitney Trail, Inyo National Forest, *Greven s.n.* (CAS); Mariposa Co.: Aqua Fria Road near Mariposa, *Congdon s.n.* (FH) [determined by Muñoz]; Mono Co.: Highway 182 at Devils Gate near Nevada State line, Toiyabe National Forest, *Greven s.n.* (CAS); Napa Co.: Napa Soda Springs, *Mann s.n.* (NY) [confirmed by Muñoz].

***Grimmia hamulosa* Lesquereux** [Grimmiaceae]

Literature: Greven 2003; Koch 1950a, 1958; Koch and Ikenberry 1954; Lesquereux 1868; Lesquereux and James 1884; Muñoz 2000; Showers 1982; Spjut 1971; Watson 1880. As *Grimmia brevirostris* Koch 1950a, 1958; Williams 1920.

Illustrations: Greven 2003.

Geographic subdivisions: CaR, SN, SNE.

Selected specimens: Fresno Co.: below Kearsarge Pass, South Fork Kings River, Kings Canyon National Park, *Shevock* 14329; Inyo Co.: slopes above Treasure Lake west of Big Pine, John Muir Wilderness, Inyo National Forest, *Norris* 47005; Mariposa Co.: Yosemite Valley, ledges near Wawona Tunnel, Yosemite National Park, *Flowers* 5413 (MO) [determined by Muñoz]; Nevada Co.: trail from Donner Rest Area to Summit Lake, Tahoe National Forest, *Whittemore* 3042 & 3045 (MO) [determined by Muñoz]; Tulare Co.: Sawtooth Pass Tail, Mineral King, Sequoia National Park, *Shevock & O'Brien* 16026 (determined by Muñoz).

***Grimmia laevigata* (Bridel) Bridel** [Grimmiaceae]

Literature: Albert 1988; Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Long 1978; McCleary 1972; Mishler 1978; Sayre 1940; Shevock and Toren 2001; Toren 1977; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Grimmia leucophaea* Kingman 1912; Lesquereux 1868; Lesquereux and James 1884; Watson 1880.

Illustrations: Crum and Anderson 1981; Flowers 1973; Greven 2003; Ignatov and Cao 1994; Ignatov and Ignatova 2003; Lawton 1971; Muñoz 1999a; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, DMoj, DSon, NW, SN, SW.

Selected specimens: Butte Co.: North Table Mountain, Cherokee Road, *Janeway* 5569 (MO) [determined by Muñoz]; Fresno Co.: Cripe Road near Patterson Road, Sierra National Forest, *Shevock & York* 14940 (determined by Muñoz); Kern Co.: Piute Mountain Road, BLM Bodfish Piute Cypress Natural Area, Piute Mountains, *Shevock* 12476; Riverside Co.: Highway 74 at milepost 76.50 near Santa Rosa Mountain Road, San Jacinto Mountains, San Bernardino National Forest, *Shevock* 20519; San Diego Co.: Matagual Creek, Volcan Mountains, *Stark* 594 (MO) [determined by Muñoz]; San Mateo Co.: Edgewood Park, Old Stage Road, *Whittemore* 5276 (MO) [determined by Muñoz]; Santa Barbara Co.: Cherry Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock* 20908 (confirmed by Muñoz).

***Grimmia leibergii* Paris** [Grimmiaceae]

Literature: Muñoz 1999b.

Illustrations: Greven 2003; Muñoz 1999b.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Alameda Co.: near Sunol Peak, *Brewer* 1492 (CAS) [determined by Toren]; Fresno Co.: Cripe Road near junction with Peterson Mill Road, Sierra National Forest, *Shevock & York* 14941 (confirmed by Bednarek-Ochyra); Glenn Co.: west of town of Elk Creek, Ivory Mill Road (20N01), 1.2 miles above junction with County Road 308, Mendocino National Forest, *Shevock* 15806; Kern Co.: Piute Cypress Botanical Area, Sequoia National Forest, *Shevock* 15502 (determined

by Bednarek-Ochyra); Lake Co.: 2 miles southwest of Lake Pillsbury, Mendocino National Forest, *Toren* 7440 (CAS) [determined by Muñoz] and Hell's Peak near Bachelor Valley, *Toren & Dearing* 6865 (CAS); Siskiyou Co.: north of Cook and Green Pass, Rogue River National Forest, *Toren & Shevock* 8233 (CAS); Tuolumne Co.: South Fork Tuolumne River at Rainbow Pool, Highway 120, Stanislaus National Forest, *Shevock* 18459 (determined by Muñoz).

***Grimmia lesherae* H. C. Greven** [Grimmiaceae]

Literature: Greven 2003.

Illustrations: Greven 2003.

Geographic subdivisions: CaR.

Selected specimens: Siskiyou Co.: Hidden Valley, Mt. Shasta, Shasta-Trinity National Forest, *Greven s.n.* (CAS).

***Grimmia lisae* De Notaris** [Grimmiaceae]

Literature: Greven 2003; Kellman 2003; Shevock and Toren 2001; Whittemore and Sommers 1999. As *Grimmia californica* Brandegees 1891; Kingman 1912; Lesquereux 1868; Lesquereux and James 1884; Moxley 1928; Sullivant 1856; Watson 1880. As *Grimmia trichophylla* var. *brachycarpa* Toren 1977.

Illustrations: Greven 2003.

Geographic subdivisions: CaR, CW, NW, SN, SW.

Selected specimens: Lake Co.: County Road to Lake Pillsbury at Dashiells Creek, Mendocino National Forest, *Toren* 7262 (CAS) [determined by Whittemore]; San Francisco Co.: Yerba Buena Island, *Toren* 8056 (CAS) and *Shevock* 19109 (determined by Muñoz); Santa Barbara Co.: Windmill Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock* 20898 (determined by Muñoz); Santa Clara Co.: north shore of Lake Grant, Lake Grant County Park, *Whittemore* 6069 (CAS, MO) [determined by Muñoz]; Tulare Co.: along flume above Ash Mountain Headquarters, Sequoia National Park, *Shevock & Morosco* 16780 (determined by Muñoz).

***Grimmia longirostris* W. J. Hooker**

[Grimmiaceae]

Literature: Muñoz 1998a.

Illustrations: Allen 2002; Greven 2003; Ignatov and Ignatova 2003; Muñoz 1998a, 1999a. As *Grimmia affinis* Ireland 1982; Lawton 1971.

Geographic subdivisions: CW, SW.

Selected specimens: Contra Costa Co.: north slope of Mt. Diablo, *Hermann* 11357 (determined by Muñoz); Marin Co.: Nicasio-Point Reyes Road, *Weber & Rundel* 48304 (MO); Orange Co.: Silverado Canyon, *Gittins* 679 (MO); San Diego Co.: Pacific Crest Trail about 9 miles from Warner Springs, *G. Allen* 648 (MO) [determined by Muñoz].

***Grimmia mariniana* Sayre** [Grimmiaceae]

Literature: Crum 1957; Greven 2003; Muñoz and Pando 2000; Sayre 1955; Toren and Sigal 1974; Yurky 1990, 1995.

Illustrations: Greven 2003; Sayre 1955.

Geographic subdivisions: CW, NW.

Selected specimens: Contra Costa Co.: Mt. Diablo below summit, *Hermann* 17360 (CAS); Lake Co.: east slope of Cobb Mountain, *Toren & Dearing* 7125 (CAS) [determined by Muñoz]; Marin Co.: Mt. Tamalpais, *Schofield* 5798 (CAN) [determined by Crum], eastside of East Peak of Mt. Tamalpais, Mt. Tamalpais State Park, *J.T. Howell s.n.* (CAS) and Rock Spring Trail, *Yurky* 483 (SFSU); Napa Co.: Mt. St. Helena, *Koch* 2125 (UC).

***Grimmia mollis* Bruch & W. P. Schimper** [Grimmiaceae]

Literature: Crum and Anderson 1981. As *Hydrogrimmia mollis* [see Muñoz and Pando 2000].

Illustrations: Crum and Anderson 1981; Greven 2003; Ignatov and Cao 1994; Lawton 1971. As *Hydrogrimmia mollis* Ignatov and Ignatova 2003.

Geographic subdivisions: SN, SNE.

Selected specimens: Fresno Co.: from Mono Pass to Golden Lake, John Muir Wilderness, Sierra National Forest, *Norris* 47022; Inyo Co.: above Chocolate Lake west of Big Pine, John Muir Wilderness, Inyo National Forest, *Norris* 46874 and George Lake west of Bishop, John Muir Wilderness, Inyo National Forest, *Norris* 71463.

***Grimmia montana* Bruch & W. P. Schimper** [Grimmiaceae]

Literature: Bourell 1981; Brandegees 1891; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Long 1978; Muñoz 1998b; Shevock and Toren 2001; Showers 1982; Sigal 1975; Spjut 1971; Strid 1974; Toren 1977; Watson 1880; Yurky 1990, 1995.

Illustrations: Greven 2003; Lawton 1971; Muñoz 1998b, 1999a; Smith 1978.

Notes: Many specimens attributed as *G. montana* in earlier references for California are actually *G. ungeri* according to Muñoz.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Fresno Co.: between Boulder Creek and Boyden Cave, Sequoia National Forest, *Shevock & York* 13644 (determined by Muñoz); Glenn Co.: St. John Mountain, Mendocino National Forest, *Shevock & Toren* 20962 (confirmed by Muñoz); Madera Co.: Nelder Redwood Grove, Sierra National Forest, *Shevock & Kellman* 19611 (determined by Muñoz); Santa Cruz Co.: Quail Hollow Ranch, *Kellman* 1142 (CAS); Tulare Co.: Elk Creek near Potwisha Campground, Middle Fork Kaweah River, Sequoia National Park, *Shevock, Norris, & Barahona* 13183.

***Grimmia moxleyi* R. S. Williams in Holzinger** [Grimmiaceae]

Literature: Greven 2003; Harthill et al. 1979; Koch 1950a; Long 1978; Moxley 1928.

Illustrations: Greven 2003.

Notes: According to Muñoz (personal communication), *Grimmia moxleyi* represents the long hair point expression of the widespread taxon *Grimmia orbicularis*. Roxanne Hastings (personal communication) and Greven (2003), however, recognize this taxon at the species level and this is how it will be treated in the Flora of North America. Regardless of circumscription, this ecological expression is common in the Mojave Desert and easily recognized in the field by the exceedingly long white hairpoints.

Geographic subdivisions: DMoj, DSon.

Selected specimens: Angeles Co.: Big Rock Creek and Devils Punchbowl, Angeles National Forest, *Moxley 1141* (NY, MO) and Tick Canyon, *MacFadden 19695* (CAS); Inyo Co.: Fall Canyon just north of Titus Canyon, Grapevine Mountains, Death Valley National Park, *Shevock, Harpel, & York 19045*.

***Grimmia nevadensis* H. C. Greven**

[Grimmiaceae]

Literature: Greven 2002.

Illustration: Greven 2002, 2003.

Notes: Although published as *Grimmia nevadense*, the wrong Latin ending was used and is changed here in accordance with Article 60, ICBN.

Geographic subdivisions: SN, SNE.

Selected specimens: Inyo Co.: Big Pine Creek, Inyo National Forest, *Greven C53* (pers. herb.); Kern Co.: Highway 178, about 2 miles east of Canebrake, Scodie Mountains, *Greven C51* (pers. herb.); Mono Co.: Devil's Gate along Highway 395, Toiyabe National Forest, *Greven C52, C54, C55* (pers. herb.); Tulare Co.: Troy Meadows, Sequoia National Forest, *Greven C50* (BM, CAS, NY, pers. herb.).

***Grimmia orbicularis* Bruch in Wilson**

[Grimmiaceae]

Literature: Muñoz 2000.

Illustrations: Flowers 1973; Greven 2003; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, DMoj, DSon, MP, SN, SNE, SW.

Selected specimens: Butte Co.: Upper Bidwell Park, Chico, *Janeway & Castro 5404* (MO) [determined by Muñoz]; Kern Co.: Rosamond Dry Lake, Mojave Desert, *MacFadden 18557 & 21917* (MO) [determined by Muñoz]; Los Angeles Co.: Devil's Punchbowl, San Gabriel Mountains, Angeles National Forest, *Moxley 1141* (MO) [determined by Muñoz]; San Bernardino Co.: Superior Valley, China Lake Naval Weapons Center, Mojave Desert, *Laeger & Silverman 875* (CAS, MA) [determined by Muñoz]; Tulare Co.: Packsaddle Creek at the base of Packsaddle Cave, Kern Plateau, Sequoia National Forest, *Shevock 10306*.

***Grimmia ovalis* (Hedwig) Lindberg**

[Grimmiaceae]

Literature: Crum and Anderson 1981; Harthill et al. 1979; Kellman 2003; McCleary 1972; Sayre 1951. As *Grimmia commutata* Lesquereux and James 1884.

Illustrations: Allen 2002; Flowers 1973; Greven 2003; Ignatov and Cao 1994; Ignatov and Ignatova 2003; Lawton 1971; Muñoz 1999a; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CW, DMoj, DSon, MP, SN, SNE.

Selected specimens: Fresno Co.: LeConte Canyon, Middle Fork Kings River, Kings Canyon National Park, *Shevock & Haultain 18626* and north of Shaver Lake along Forest Highway 8, Sierra National Forest, *Shevock & Norris 19794* (determined by Muñoz); Inyo Co.: South Fork Hanaupah Canyon, east base of Telescope Peak, Death Valley National Park, *Shevock & York 21358*; Mariposa Co.: Highway 120 near Yosemite Creek Campground, Yosemite National Park, *Shevock 18483* (determined by Muñoz); Santa Cruz Co.: China Grade, Big Basin Redwoods State Park, *Kellman 1293* (CAS, MA) [determined by Muñoz]; Tulare Co.: lower end of Crabtree Meadows west of Mt. Whitney, Sequoia National Park, *Shevock 18549* (determined by Muñoz); Tuolumne Co.: Highway 108, 6.1 miles east of Mi-Wok Ranger Station, Stanislaus National Forest, *Shevock 18587* (determined by Muñoz).

***Grimmia plagiopodia* Hedwig** [Grimmiaceae]

Literature: Coville 1893; Crum and Anderson 1981; Flowers 1973; Holzinger 1922; Koch 1950a, 1951e; Showers 1982; Wynne 1943.

Illustrations: Crum and Anderson 1981; Flowers 1973; Greven 2003; Ignatov and Cao 1994; Ignatov and Ignatova 2003; Lawton 1971; Muñoz 1999a.

Geographic subdivisions: CaR, DMoj, SN, SNE.

Selected specimens: Amador Co.: Highway 88 at Silver Lake, Eldorado National Forest, *Showers 3300* (CAS, SFSU) [confirmed by Toren]; Inyo Co.: about 2 miles south of Tucki Mountain, Tucki Mountain Wilderness, Death Valley National Park, *Laeger 924* (CAS, MA) [determined by Muñoz]; San Bernardino Co.: Eagle Crags, China Lake Naval Weapons Center, Mojave Desert, *Laeger & Silverman 883* (CAS, MA) [determined by Muñoz]; Tehama Co.: Mt. Conard, Lassen Volcanic National Park, *Showers 3717* (CAS, SFSU) [confirmed by Toren].

****Grimmia poecilostoma* Cardot & Seblle**

[Grimmiaceae]

Illustrations: Greven 2003; Muñoz 1999a.

Notes: According to Muñoz (personal communication) without sporophytes, this taxon is morphologically indistinguishable from *G. tergestina*.

Geographic subdivisions: CaR, CW, DMoj, NW, SN, SNE.

Selected specimens: Contra Costa Co.: Mitchell Canyon, Mt. Diablo State Park, *Norris 100616*; Inyo Co.: Porter Peak, Panamint Mountains, Death Valley National Park, *Laeger 926* (CAS, MA) [determined by Muñoz]; Madera Co.: Beashore Road near Portuguese Creek southwest of the Balls, Sierra National Forest, *Shevock & Kellman 19681* (determined by Muñoz); San Bernardino Co.: Victorville, *Braun s.n.* (MO) [determined by Muñoz]; Siskiyou Co.: Forest Road 40N56, southeast slope of Mt. Shasta, Shasta-Trinity National Forest, *Norris & Hillyard 104077*.

***Grimmia pulvinata* (Hedwig) J. E. Smith**
[Grimmiaceae]

Literature: Bourell 1981; Bradshaw 1926; Cooke 1941; Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Koch 1949a, 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Long 1978; McCleary 1972; Mishler 1978; Shevock and Toren 2001; Spjut 1971; Steere 1954; Steere et al. 1954; Toren 1977; Watson 1880; Yurky 1990, 1995.

Illustrations: Crum and Anderson 1981; Flowers 1973; Greven 2003; Ignatov and Ignatova 2003; Lawton 1971; Muñoz 1999a; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, DMOj, NW, SN, SW.

Selected specimens: Fresno Co.: Kings River Trail, Sierra National Forest, *Shevock & York 12368*; Lake Co.: Clear Lake State Park, *Toren 6840* (CAS); Mendocino Co.: Indian Creek County Park near Philo, *Norris 53235*; Riverside Co.: south of Twentynine Palms at county line, *Norris 57964*; San Francisco Co.: Yerba Buena Island, San Francisco, *Shevock 19113*; Santa Barbara Co.: Miranda Pine Mountain, Los Padres National Forest, *Norris 55314*; Siskiyou Co.: Idlewild Campground about 10 miles east of Sawyers Bar on road to Etna, Klamath National Forest, *Norris 11838*; Tuolumne Co.: Forest Road 17 near Cherry Creek Bridge, Stanislaus National Forest, *Shevock & Ertter 19551* (determined by Muñoz).

***Grimmia ramondii* (Lamarck & A. P. de Candolle) Margadant** [Grimmiaceae]

Literature: See Muñoz and Pando 2001. As *Dryptodon patens* Crum and Anderson 1981; Showers 1982; Vitt and Belland 1991. As *Racomitrium patens* Holmberg 1969; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; McGrew 1976; Spjut 1971.

Illustrations: Crum and Anderson 1981; Greven 2003; Ignatov and Ignatova 2003; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, MP, NW, SN.

Selected specimens: Del Norte Co.: Whiskey Lake, Six Rivers National Forest, *Norris 83362*; Lake Co.: Stony Creek, Snow Mountain Wilderness, Mendocino National Forest, *Toren & Dearing*

5344 (CAS); Modoc Co.: road to Beeler Reservoir about 16 miles east of Medicine Lake, Modoc National Forest, *Norris 22506*; Nevada Co.: Fall Creek between Bowman Lake and Highway 20, Tahoe National Forest, *Shevock, Ertter, & Morosco 15708* (determined by Muñoz); Placer Co.: North Fork Campground southeast of Emigrant Gap, *Norris 88042 & 88043*; Shasta Co.: Coffee Creek at East Fork of Coffee Creek, *Norris & Hermann 22578*; Siskiyou Co.: Etna-Sawyers Bar Road about 18 miles from Etna, *Norris & Hermann 22745* and Baldy Mountain above Happy Camp, Klamath National Forest, *Branscomb 22739* (MO) [determined by Muñoz]; Tehama Co.: Doll Basin Research Natural Area, Mendocino National Forest, *Toren & Bourell 6792* (CAS, MO).

***Grimmia reflexidens* C. Müller Hal.**
[Grimmiaceae]

Literature: Muñoz 1998b. As *Grimmia sessitana* Greven 2003. As *Grimmia tenerrima* Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Long 1978; McGrew 1976; Mishler 1978; Showers 1982.

Illustrations: Crum and Anderson 1981; Greven 2003; Ignatov and Ignatova 2003; Muñoz 1998b, 1999a; Ochrya 1998a; Sharp et al. 1994.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Fresno Co.: between Swede and Mystery Lake, Dinkey Lakes Wilderness, Sierra National Forest, *Shevock & York 13916* (determined by Muñoz); Lake Co.: near summit of West Peak, Snow Mountain Wilderness, Mendocino National Forest, *Toren & Dearing 7478* (CAS) [determined by Muñoz]; Madera Co.: north of Quartz Mountain Trailhead, Sierra National Forest, *Shevock & Kellman 19641* (determined by Muñoz); Mariposa Co.: above Half Moon Meadow toward Ten Lakes, Yosemite National Park, *Shevock 19494* (determined by Muñoz); Plumas Co.: about 2 miles east of Blairsden, *J.T. Howell s.n.* (MO) [determined by Muñoz]; Tehama Co.: Tomhead Gulch, Shasta-Trinity National Forest, *Norris 56899*; Tulare Co.: Lloyd Meadows Basin, Sequoia National Forest, *Shevock 4014*.

***Grimmia serrana* Muñoz, Shevock & Toren**
[Grimmiaceae]

Literature: Greven 2003; Muñoz et al. 2002.

Illustrations: Greven 2003; Muñoz et al. 2002.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Amador Co.: off of Highway 26 above North Fork Mokelumne River about 2 miles north of West Point, *Toren 8669* (CAS); Butte Co.: Big Bald Rock about 3 miles south of Brush Creek Work Center east of Lake Oroville, Plumas National Forest, *Toren s.n.* (CAS); Calaveras Co.: Winton Road, 3.9 miles northeast of West Point, *Toren 8668* (CAS); Fresno Co.: Peterson Mill Road west of Soaproot Saddle, Sierra National Forest, *Shevock, York, & Clines 14975a* and Mist Falls Trail, Kings Canyon National Park, *Shevock*

& *York 14479* (determined by Muñoz); Kern Co.: Kern River Road (old Highway 178) near Bodfish, Sequoia National Forest, *Shevock 14871*; Lake Co.: Big Rock north of Deer Valley east of Elk Mountain, Mendocino National Forest, *Toren 8002* (CAS, MA) [confirmed by Muñoz] and *Toren & Dearing 8657* (CAS, MA, MO, NY, UC); Madera Co.: along Forest Highway 81 between Rock and Slide Creeks, Sierra National Forest, *Norris & Shevock 100060*; Mariposa Co.: Merced River above El Portal entrance, Yosemite National Park, *Shevock & Norris 20164*; Placer Co.: Dutch Flat, *MacFadden 3840* (MO) [determined by Muñoz] and Highway 20, east end of Bear Flat, Tahoe National Forest, *Shevock & Toren 20707*; Tulare Co.: Wishon Campground, North Fork of Middle Fork Tule River, Sequoia National Forest, *Shevock & Morosco 16808* (determined by Muñoz).

***Grimmia shastae* H. C. Greven** [Grimmiaceae]

Literature: Greven 2003.

Illustrations: Greven 2003.

Notes: Although published as *Grimmia shastai*, the wrong Latin ending was used and is changed here in accordance with Article 60, ICBN.

Geographic subdivisions: CaR.

Selected specimens: Siskiyou Co.: Mt. Shasta, Shastina Peak, *W. B. Cooke 18282* (CAS, MICH).

****Grimmia tergestina* Tommasini ex Bruch & W. P. Schimper.** [Grimmiaceae]

Illustrations: Greven 1999c, 2003; Ignatov and Cao 1994; Ignatov and Ignatova 2003; Muñoz 1999a.

Notes: According to Muñoz (personal communication) without sporophytes, this taxon is morphologically indistinguishable from *G. poecilostoma*.

Geographic subdivisions: DMOj, NW, SN.

Selected specimens: Kern Co.: Chimney Creek Road, Kern Plateau, *Shevock 15170* and Sand Canyon north of Tehachapi, *Hare 238* (CAS, MA) [determined by Muñoz]; Lake Co.: Forest Road M-1 at Eel River Bridge near Lake Pillsbury, Mendocino National Forest, *Toren & Dearing 7357* (CAS) [determined by Muñoz] and Hell's Peak near Blue Lakes, *Toren & Dearing 6857* (CAS) [determined by Muñoz] and Hell's Peak north of Bachelor Valley *Toren 778* (SFSU, UC).

***Grimmia torquata* Drummond** [Grimmiaceae]

Literature: Crum and Anderson 1981; Holmberg 1969; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; McGrew 1976; Showers 1982; Spjut 1971; Toren 1977; Yurky 1990, 1995.

Illustrations: Crum and Anderson 1981; Greven 2003; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN, SNE.

Selected specimens: Del Norte Co.: Poker Creek, Illinois River, Siskiyou National Forest, *Shevock & Toren 20144*; Humboldt Co.: Bear Butte, *Brancomb & Grunman 22828* (MO) [determined by

Muñoz]; Fresno Co.: Forest Highway 5 at Kaiser Creek, Sierra National Forest, *Shevock & Norris 19833*; Lake Co.: Forest Road M-1 at Eel River Bridge, Mendocino National Forest, *Toren 5051* (CAS); Marin Co.: Bootjack Trail, Mt. Tamalpais State Park, *Yurky 332* (SFSU); Mariposa Co.: Yosemite Falls, Yosemite National Park, *MacFadden 17442* (MO) and Vernal Falls, *MacFadden 17441* (MO) [determined by Muñoz]; Placer Co.: Dutch Flat, *MacFadden 16994* (MO) [determined by Muñoz]; Tulare Co.: Crystal Cave Road at junction with Little Deer Creek, Sequoia National Park, *Shevock & Tseng 15774*.

***Grimmia trichophylla* Greville** [Grimmiaceae]

Literature: Bourell 1981; Bradshaw 1926; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Kingman 1912; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Long 1978; McCleary 1972; McGrew 1976; Millspaugh and Nuttall 1923; Mishler 1978; Sayre 1940; Shevock and Toren 2001; Showers 1982; Sigal 1975; Smith 1970; Spjut 1971; Steere 1954; Steere et al. 1954; Strid 1974; Sullivant 1856; Toren 1977; Yurky 1990, 1995. As *Grimmia trichophylla* var. *meridionalis* Koch 1950a; Lesquereux and James 1884. As *Grimmia ancistrodes* Lesquereux 1868. As *Grimmia watsoni* Brandegees 1891; Lesquereux and James 1884. Misapplied as *Grimmia trichophylla* var. *muehlenbeckii* Koch 1950a; Lesquereux and James 1884. Misapplied as *Grimmia muehlenbeckii* Lesquereux 1868; Lesquereux and James 1884. Misapplied as *Grimmia decipiens* Holmberg 1969; Koch 1950a; McCleary 1972; Sayre 1940; Spjut 1971.

Illustrations: Greven 2003; Lawton 1971; Muñoz 1999a; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN, SW.

Selected specimens: Kern Co.: Pacific Crest Trail 2 miles south of Walker Pass, Sequoia National Forest, *Shevock 13373* (determined by Muñoz); Fresno Co.: LeConte Canyon, Kings Canyon National Park, *Shevock & Haultain 18630* (determined by Muñoz); Lake Co.: Mt. Sanhedrin, Mendocino National Forest, *Shevock, Ertter, Toren, & Dearing 19478* (determined by Muñoz); Tehama Co.: north slope of Tedoc Mountain, Shasta-Trinity National Forest, *Shevock & Ertter 19382* (determined by Muñoz); Tulare Co.: Elk Creek near Potwisha Campground, Middle Fork Kaweah River, Sequoia National Park, *Shevock, Norris, & Barahona 13191a*; Tuolumne Co.: Columns of the Giants Geological Area, Stanislaus National Forest, *Shevock 18591* (determined by Muñoz).

***Grimmia ungeri* Juratzka in Unger & Kotschy** [Grimmiaceae]

Literature: Kellman 2003; Muñoz 1998b.

Illustrations: Greven 1994, 2003; Muñoz 1998b, 1999a.

Notes: There is disagreement between Greven and

Muñoz on the status of plants attributed to be this species for California. Greven (2003) is of the opinion that *Grimmia ungeri* is restricted to southern Europe. Muñoz believes that *Grimmia ungeri* has a broader world distribution based on California specimens that he has studied.

Geographic subdivisions: CW, NW, SN.

Selected specimens: Glenn Co.: St. John Mountain, Mendocino National Forest, *Shevock & Toren 20970* (determined by Muñoz); Humboldt Co.: Horse Mountain Ski Lift, *Norris 70634*; Madera Co.: northwest base of Fresno Dome, Sierra National Forest, *Shevock & Kellman 19619* (determined by Muñoz); Mariposa Co.: Half Moon Meadow toward Ten Lakes, Yosemite National Park, *Shevock 19495* (determined by Muñoz); Santa Barbara Co.: Figueroa Mountain Road east of Los Olivos, *Norris 103635*; Santa Cruz Co.: Quail Hollow County Park, *Kellman 120* (CAS) [determined by Muñoz]; Tehama Co.: slope of Tedoc Mountain, Shasta-Trinity National Forest, *Shevock & Ertter 19383* (determined by Muñoz); Tulare Co.: Baker Point Botanical Area, Greenhorn Mountains, Sequoia National Forest, *Shevock 18400* (determined by Muñoz).

***Gymnostomum calcareum* Nees & Hornschuch**
[Pottiaceae]

Literature: Kingman 1912; Harthill et al. 1979; Koch 1950a; Koch and Ikenberry 1954; Lesquereux 1868; Long 1978; Mishler 1978; Sullivant 1856; Thomson and Ketchledge 1958; Toren 1977. As *Gymnostomum calcareum* var. *perpusillum* Brandegee 1891; Lesquereux and James 1884; Watson 1880. As *Gymnostomum aeruginosum* Crum and Anderson 1981; Kellman 2003; Lawton 1971; Shevock and Toren 2001; Showers 1982; Spjut 1971; Stark and Whittemore 1992; Toren 1977; Zander 1977a.

Illustrations: Crum and Anderson 1981; Smith 1978.

Notes: Although generally treated within the circumscription of *Gymnostomum aeruginosum* by some authors, plants attributed to *G. calcareum* are ecologically and morphologically distinctive based on our field experience. All California *Gymnostomum* collections examined are *G. calcareum*.

Geographic subdivisions: CaR, CW, DMoj, DSon, NW, SN, SW.

Selected specimens: Humboldt Co.: near Trinidad Bay, *Duell s.n.* (UC); Monterey Co.: Pinnacles, Hunter-Liggett Military Reservation, *Norris 87277*; Sonoma Co.: Cedars north of Cazadero, headwaters of Big Austin Creek, *Ertter & Raiche 12862* (UC); Tehama Co.: bluff overlooking Battle Creek near Manton, *Norris 21339*; Trinity Co.: Highway 299, 0.25 miles east of Del Loma, Shasta-Trinity National Forest, *Silver 882* (UC); Tulare Co.: Highway 190, 1.7 miles west of Pierpoint Springs, Middle Fork Tule River, Sequoia National Forest, *Shevock 10142* and Kaweah River below Ash Mountain

Headquarters, Sequoia National Park, *Shevock & Whitmarsh 17023*.

****Hamatocaulis vernicosus* (Mitten) Hedenäs**
[Campyliaceae]

Illustrations: Buck 1998; Hedenäs 1989b, 1993a, 2003. As *Drepanocladus vernicosus* Ireland 1982; Janssens 1983; Kanda 1978; Lawton 1971; Smith 1978; Wynne 1944.

Geographic subdivisions: CaR, SN, SNE.

Selected specimens: El Dorado Co.: Grass Lake along Highway 89 west of Luther Pass, *Norris 71311*; Mariposa Co.: Summit Meadow, Glacier Point Road, Yosemite National Park, *Norris & Shevock 100302*; Mono Co.: Virginia Lakes Basin at Cooney Lake, Toiyabe National Forest, *Janeway 7660* (UC); Plumas Co.: Kanaka Flat, Plumas National Forest, *Janeway 6894* (CSUC, UC).

***Hedwigia detonsa* (Howe) W. R. Buck & Norris**
[Hedwigiaceae]

Literature: Buck and Norris 1996. As *Hedwigia albicans* var. *detonsa* Howe 1897. As *Hedwigia albicans* Howe 1897; Kingman 1912. Misapplied in California as *Hedwigia ciliata* Bourell 1981; Harpel 1980a; Harthill et al. 1979; Koch 1950a; Koch and Ikenberry 1954; Lesquereux 1868; Moxley 1928; Sigal 1975; Toren 1977; Watson 1880; Yurky 1990, 1995.

Illustrations: Buck and Norris 1996.

Notes: References for *Hedwigia ciliata* in California are common prior to the revision of the North American material (Buck and Norris 1996). *Hedwigia ciliata* is actually north and east of the state and should be deleted as a component of the state bryoflora. *Hedwigia detonsa* is widespread and generally inland in distribution, whereas *Hedwigia stellata* is generally more coastal.

Geographic subdivisions: NW, SN, SW.

Selected specimens: Alameda Co.: upper boundary of Bidwell Park, *Norris 70096*; San Diego Co.: Highway 76 at west edge of Cleveland National Forest, *Norris 70198*; San Luis Obispo Co.: west of roads to Black Mountain and Navajo Camp, *Norris 55252*; Shasta Co.: Highway 44 at Bear Creek, *Norris 52775*; Tulare Co.: Elk Creek near Potwisha Campground, Middle Fork Kaweah River, Sequoia National Park, *Shevock, Norris, & Barahona 13190*.

***Hedwigia stellata* Hedenäs** [Hedwigiaceae]

Literature: Buck and Norris 1996; Kellman 2003. [See notes for *Hedwigia detonsa*.]

Illustrations: Buck and Norris 1996.

Geographic subdivisions: CaR, CW, NW, SN, SW.

Selected specimens: Contra Costa Co.: Castle Rocks, Mt. Diablo State Park, *Shevock & Ertter 20354*; El Dorado Co.: Sopiago Creek southeast of Placerville, Eldorado National Forest, *Norris 67187*; Humboldt Co.: Bald Hills Road at Coyote Peak, *Norris 22333*; Lake Co.: Mt. Konocti just below Buckingham Bluffs, *Shevock, Heise, Harpel, &*

Toren 20598; Los Angeles Co.: Santa Anita Canyon, San Gabriel Mountains, Angeles National Forest, *Moxley 994* (MO); Monterey Co.: Arroyo Seco Road near Carmel River, *Toren & Showers 2883* (SFSU); Riverside Co.: Cahuilla Mountain above Tripps Flat, *Shevock 20532*; Santa Cruz Co.: Eagle Rock, *Kellman 1272* (CAS); Shasta Co.: Fall Creek Road, 1 mile southeast of McCloud Bridge, Shasta Lake, *Norris 84860*.

****Helodium blandowii* (Weber & D. Mohr) Warnstorf** [Helodiaceae]

Illustrations: Abramov and Volkova 1998; Abramova and Abramov 1972; Flowers 1973; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: SN, SNE.

Selected specimens: Fresno Co.: Kings Canyon National Park, Middle Fork Kings River, Big Pete Meadow about 2 miles up canyon from LeConte Ranger Station, *Shevock, Haultain, & Hayden 18663* and between Grouse Meadow and LeConte Ranger Station, *Shevock & Haultain 18635*; Mono Co.: between Rock Creek Lake and Hilton Creek Lakes, Inyo National Forest, *Shevock & Toren 21461* and 0.5 mile north of Davis Lake, Inyo National Forest, *Weis 371* (UC) and East Fork Swauger Creek east of Devils Gate and north of Bridgeport, Toiyabe National Forest, *Norris 104239*.

***Hennediella heimii* (Hedwig) Zander** [Pottiaceae]

Literature: Kellman 2003; Shevock and Toren 2001. As *Pottia heimii* Flowers 1973; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Watson 1880. As *Desmatodon heimii* Crum and Anderson 1981; Toren 1977.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Ochrya 1998a; Smith 1978; Zander 1993.

Geographic subdivisions: CW, MP, NW, SNE.

Selected specimens: Contra Costa Co.: Mt. Diablo State Park, *Norris 100551*; Inyo Co.: Rock Creek, *MacFadden 18579* (MO); Lake Co.: north end of Bachelor Valley near Hell's Peak, *Toren 839* (CAS, SFSU) [confirmed by Zander]; Mendocino Co.: location not specified beyond T12N R13W sections 21–23, *Hamilton s.n.* (UC); San Francisco Co.: Letterman Hospital Complex, Presidio of San Francisco, *Shevock 20207*; Santa Cruz Co.: Yellow Bank Creek, *Kellman 2107* CAS); Shasta Co.: Highway 299 east of Burney at milepost 83, *Norris 21512*.

***Hennediella stanfordensis* (W. C. Steere) Blockeel** [Pottiaceae]

Literature: Kellman 2003; Shevock and Toren 2001. As *Tortula stanfordensis* Blockeel 1990; Crum 1957; Koch and Ikenberry 1954; Steere 1951; Toren 1977; Whitehouse 1971; Yurky 1990, 1995.

Illustrations: Sharp et al. 1994; Smith 1978; Steere 1951; Whitehouse and Newton 1988; Zander 1993.

Geographic subdivisions: CW, GV, NW, SN.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris 87167 & 87180*; Humboldt Co.: Humboldt County Courthouse, Eureka, *Norris s.n.*; Mariposa Co.: Cathey's Valley Cemetery along Highway 140 about 11 miles west of Mariposa, *Norris 80863*; Merced Co.: along County Road J-16 about 0.5 mile east of Snelling along Merced River, *Norris 69850*; San Francisco Co.: Potrero Hill, *Toren 7827* (CAS); Santa Cruz Co.: Highway 9 near Highway 35, *Kellman 664* (CAS); Tulare Co.: Clough Cave, South Fork Kaweah River, Sequoia National Park, *Norris 92737*.

***Herzogiella seligeri* (Bridel) Iwatsuki** [Hypnaceae]

Literature: Spjut 1971.

Illustrations: Ignatov et al. 1996. As *Isopterygium seligeri* Lawton 1971.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: Sanger Lake along Forest Road 4803 southeast of O'Brien, Six Rivers National Forest, *Norris 70810*; Humboldt Co.: Forest Road 10N02 at head of Mill Creek, Six Rivers National Forest, *Norris 70601*; Siskiyou Co.: Haypress Meadows, Marble Mountain Wilderness, Klamath National Forest, *Norris 12401*.

***Herzogiella striatella* (Bridel) Iwatsuki** [Hypnaceae]

Literature: Spjut 1971.

Illustrations: Ireland 1982; Smith 1978.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: slopes above Sanger Lake southeast of O'Brien, Six Rivers National Forest, *Norris 70856*; Humboldt Co.: upper reaches of Marshall Creek, *Norris 56689*; Siskiyou Co.: Bear Lake, *Norris 24211 & 21217*.

***Heterocladium dimorphum* (Bridel) Bruch & W. P. Schimper** [Pterigynandraceae]

Literature: Shevock and Toren 2001.

Illustrations: Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CW.

Selected specimens: San Francisco Co.: Lafayette Park, *Shevock 19242 & 19245* and Balboa Park, *Shevock 19279*.

***Heterocladium macounii* Best** [Pterigynandraceae]

Literature: Bourell 1981. As *Heterocladium heteropteroides* Koch 1950a.

Illustrations: Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: Smith River along Highway 199, Jedediah Smith Redwood State Park, *Norris 68934*; Humboldt Co.: near Prairie Creek Campground, Prairie Creek Redwood State Park, *Norris 12030* and Highway 299 at mile 9.4 east of Arcata, *Norris 55074*; Trinity Co.: Onion

Lake Road about 7 miles south of Onion Lake, *Norris* 72549 & 72562.

***Homalothecium aeneum* (Mitten) E. Lawton**

[Brachytheciaceae]

Literature: Harpel 1980a; Harthill et al. 1979; Lawton 1965a, 1971; McCleary 1972; Spjut 1971; Toren 1977. As *Camptothecium aeneum* Koch 1950a; Steere 1954. As *Camptothecium aeneum* var. *dolosum* Sayre 1940. As *Camptothecium dolosum* Millspaugh and Nuttall 1923.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, CW, MP, SN, SW.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris* 87169; Colusa Co.: Indian Valley Lake, Mendocino National Forest, *Norris* 67547; Fresno Co.: near Boyden Cave, Monarch Wilderness, Sequoia National Forest, *Shevock & York* 12335; Lake Co.: Clear Lake State Park, *Norris* 47719; Lassen Co.: Aspen Grove Campground, south end of Eagle Lake, *Norris* 52816; Santa Barbara Co.: Bates Canyon, Cole Springs Campground, *Norris* 55323; Trinity Co.: Hall City Caves east of Wildwood, Shasta-Trinity National Forest, *Norris* 71661; Ventura Co.: Lower San Juan Picnic Area, *Norris* 58156.

***Homalothecium arenarium* (Lesquereux) E.**

Lawton [Brachytheciaceae]

Literature: Harthill et al. 1979; Jamieson 1969; Kellman 2003; Lawton 1965a, 1971; Long 1978; McCleary 1972; Shevock and Toren 2001; Spjut 1971; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Camptothecium alsoides* Kindberg 1892; Koch 1950a; Steere 1954. As *Camptothecium arenarium* Howe 1896; Kingman 1912; Koch 1950a; Millspaugh and Nuttall 1923; Sayre 1940; Steere 1954. As *Hypnum arenarium* Brandegees 1891; Lesquereux 1868; Watson 1880.

Illustrations: Lawton 1965a, 1971; Sharp et al. 1994.

Geographic subdivisions: CaR, CW, NW, SN, SW.

Selected specimens: Lake Co.: base of Mt. Konocti, Clear Lake State Park, *Toren* 7039 (CAS); Mariposa Co.: Moss Canyon near El Portal, Yosemite National Park, *Norris* 80894; Riverside Co.: Mesa de Colorado, Santa Rosa Plateau Preserve west of Murrieta, *Weber, Bratt & Larson* 91958 (UC); San Francisco Co.: Baker Beach, Presidio of San Francisco, *Shevock* 18948; Santa Barbara Co.: Water Canyon east of Black Mountain, Santa Rosa Island, Channel Islands National Park, *Shevock & Rodriguez* 20819; Sonoma Co.: Wolf Creek Road about 4 miles east of Gualala River, *Norris* 86946; Tehama Co.: Highway 36 about 5 miles northeast of Red Bluff, *Norris* 48076; Tulare Co.: General's Highway at Four Guardsman, Giant Forest, Sequoia National Park, *Rundel* 3082 (UC).

***Homalothecium fulgens* (Mitten ex C. Müller**

Hal.) E. Lawton [Brachytheciaceae]

Literature: Holmberg 1969; Jamieson 1969; Lawton 1965a, 1971; Spjut 1971. As *Camptothecium*

lutescens var. *occidentale* Howe 1896; Koch 1950a; Yurky 1990, 1995. As *Camptothecium lutescens* var. *fulgens* Koch and Ikenberry 1954. As *Hypnum lutescens* Lesquereux 1868.

Illustrations: Lawton 1965a, 1971; Smith 1978.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: El Dorado Co.: Sopiago Creek, southeast of Placerville, *Norris* 67201; Humboldt Co.: shores of Lake Prairie, *Norris* 50402; Lassen Co.: Battle Creek at milepost 75, *Norris* 52685; Mendocino Co.: Mill Creek County Recreation Area about 8 miles east of Ukiah, *Norris* 72627; Plumas Co.: Highway 36 at Gurnsey Creek east of Mineral, *Norris* 48129; Shasta Co.: Highway 299 about 1 mile north of Mineral School at intersection of road to Oak Run, *Norris* 68626; Siskiyou Co.: Shadow Creek at Callahan to Cecilville Road about 6 miles northeast of Cecilville, *Norris* 70542.

***Homalothecium nevadense* (Lesquereux)**

Renauld & Cardot [Brachytheciaceae]

Literature: Flowers 1973; Harpel 1980a; Harthill et al. 1979; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1965a, 1971; Long 1978; McGrew 1976; Mishler 1978; Sigal 1975; Spjut 1971; Steere et al. 1954; Strid 1974; Toren 1977; Yurky 1990, 1995. As *Hypnum nevadense* Lesquereux 1868; Watson 1880. As *Camptothecium nevadense* Howe 1896.

Illustrations: Flowers 1973; Lawton 1965a, 1971.

Geographic subdivisions: CaR, CW, DMOj, MP, NW, SN, SNE, SW.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris* 87192; Glenn Co.: Cottonwood Glade, *Norris* 47959; Modoc Co.: Boles Creek southeast of Clear Lake, Modoc National Forest, *Norris* 79176; Mono Co.: near Green Lake, Hoover Wilderness, Toiyabe National Forest, *Norris* 57241; Monterey Co.: Nacimiento-Ferguson Road at bridge, Hunter-Liggett Military Reservation, *Norris* 87340; Riverside Co.: McCall Park near Mountain Center east of Hemet, *Norris* 58081; San Benito Co.: Cantua Creek, BLM Clear Creek Recreation Area, *Shevock, Norris, & Hamon* 20297; Shasta Co.: Cassel-Fall River Road about 1 mile east of Shasta-Trinity National Forest boundary, *Norris* 84687; Tulare Co.: County Road M-99 at Limestone Campground, North Fork Kern River, Sequoia National Forest, *Shevock, Norris, & Barahona* 13023; Tuolumne Co.: Highway 120 west of Yosemite, Stanislaus National Forest, *Koch* 1663 (UC).

***Homalothecium nuttallii* (Wilson) A. Jaeger**

[Brachytheciaceae]

Literature: Bourell 1981; Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1965a, 1971; McCleary 1972; Shevock and Toren 2001; Sigal 1975; Smith 1970; Spjut 1971; Steere 1954; Strid 1974; Thomson and Ketchledge 1958; Toren

1977; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Camptothecium nuttallii* Bradshaw 1926. As *Hypnum nuttallii* Lesquereux 1868; Sullivant 1856. As *Hypnum nuttallii* var. *stoloniferum* Lesquereux 1868; Watson 1880.

Illustrations: Lawton 1965a, 1971.

Geographic subdivisions: CW, GV, NW, SN, SW.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris* 87201; El Dorado Co.: Bear Creek Picnic Area southeast of Georgetown, *Norris & Piippo* 82324; Los Angeles Co.: Santa Catalina Island, *G. Wheeler* 6154 (UC); Merced Co.: along County Road J16 adjacent to Merced River about 0.5 mile east of Snelling, *Norris* 69856; Monterey Co.: Arroyo Seco Creek about 4 miles west of Greenfield, *Norris* 48511; San Francisco Co.: Panhandle, Golden Gate Park, San Francisco, *Shevock* 18768; Sonoma Co.: South Ridge Trail above Lake Sonoma at Skaggs Spring Road, *Norris* 86929; Trinity Co.: South Fork Road along South Fork Trinity River, *Norris* 72837.

***Homalothecium pinnatifidum* (Sullivant & Lesquereux) E. Lawton [Brachytheciaceae]**

Literature: Bourell 1981; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Lawton 1965a, 1971; Long 1978; McCleary 1972; Sigal 1975; Spjut 1971; Toren 1977; Yurky 1990, 1995. As *Camptothecium amesiae* Howe 1897; Koch 1950a, 1951a; Koch and Ikenberry 1954; Renaud and Cardot 1888. As *Camptothecium pinnatifidum* Bradshaw 1926; Howe 1896; Kingman 1912; Koch 1950a; Koch and Ikenberry 1954; Steere 1954; Thomson and Ketchledge 1958. As *Hypnum pinnatifidum* Lesquereux 1868; Watson 1880. Misapplied as *Homalothecium aureum* Hofman 1998; Whittemore and Sommers 1999.

Illustrations: Lawton 1965a, 1971; Sharp et al. 1994.

Geographic subdivisions: CaR, CW, NW, SN, SW.

Selected specimens: Butte Co.: near Cherokee, *Norris* 73603; Kern Co.: Piute Mountain Road, BLM Bodfish Piute Cypress Natural Area, Piute Mountains, *Shevock* 12495; Mendocino Co.: Eel River about 3 miles south of Piercy, *Norris* 72111; San Diego Co.: Highway 76, Cleveland National Forest, *Norris* 70201; Santa Clara Co.: Mine Hill Trail south of Cape Horn Pass, Almaden Quicksilver County Park, *Whittemore* 5316 (UC); Santa Cruz Co.: trail to Buzzards Lagoon, Forest of Nisene Marks State Park, *Kellman* 732 (CAS); Trinity Co.: Highway 299 about 4 miles west of Weaver-ville, *Norris* 73524.

****Homomallium mexicanum* Cardot [Hypnaceae]**

Illustrations: Sharp et al. 1994.

Geographic subdivisions: DMoj.

Selected specimens: San Bernardino Co.: Curtis Canyon, Clark Mountain Wilderness, Mojave National Preserve, Mojave Desert, *Shevock, Spence, Glazer, & Laeger* 23681.

***Hookeria lucens* (Hedwig) J. E. Smith [Hookeriaceae]**

Literature: Jamieson 1969; Koch 1950a; Lawton 1971. Misapplied as *Hookeria acutifolia* Lesquereux 1868; Watson 1880. As *Pterygophyllum lucens* Howe 1897.

Illustrations: Lawton 1971.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: Damnation Creek Trail, Del Norte Redwoods State Park, *Norris & Taranto* 10989; Humboldt Co.: Emerald Creek at junction with Redwood Creek, Redwood National Park, *Norris* 45837; Mendocino Co.: County Road 409 about 1 mile east of Highway 1 south of Fort Bragg, *Norris* 11702 and Marchantia Glen, Jackson State Forest, *Bourell* 790 (CAS); Siskiyou Co.: Sugar Creek and Sugar Lake west of Callahan, Klamath National Forest, *Norris* 57327.

***Hygroamblystegium tenax* (Hedwig) Jennings [Amblystegiaceae]**

Literature: Harthill et al. 1979; Koch 1950a; Showers 1982; Strid 1974; Toren 1977. As *Amblystegium irriguum* Howe 1897; Kingman 1912. As *Amblystegium tenax* Flowers 1973. As *Hygroamblystegium irriguum* Steere et al. 1954.

Illustrations: Flowers 1973; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Del Norte Co.: border of Klamath River northwest of Orick, *R. & I. Duell* 52 (UC); Humboldt Co.: Quinby Creek about 3 miles north of Denny, Shasta-Trinity National Forest, *Norris* 52710; Inyo Co.: Forest Road 8S02 toward North Lake near Bishop Creek at Sabrina Basin, Inyo National Forest, *Shevock* 15287; Lake Co.: Anderson Springs south of Cobb Mountain, *Toren* 7164 (CAS); Sierra Co.: Highway 49 about 7.8 miles west of Sierra City, Tahoe National Forest, *Tavares & Noack* 602a (UC); Siskiyou Co.: Crawford Creek at Klamath River, Klamath National Forest, *Norris* 10493; Tulare Co.: Forks of the Kern River, Golden Trout Wilderness, Sequoia National Forest, *Shevock* 14271.

***Hygrohypnum alpinum* (Lindberg) Loeske [Campyliaceae]**

Literature: Jamieson 1976.

Illustrations: Jamieson 1976.

Geographic subdivisions: NW, SN, SNE.

Selected specimens: Fresno Co.: between Golden Lake and Mono Pass, Sierra National Forest, *Norris* 47042 (determined by Jamieson); Mono Co.: Barney Lake, Toiyabe National Forest, *Norris* 67145; Siskiyou Co.: Duck Lake Creek at Forest Road 8, Klamath National Forest, *Norris* 23300 (determined by Jamieson).

***Hygrohypnum bestii* (Renaud & Bryhn) Brotherus [Campyliaceae]**

Literature: Flowers 1973; Ireland 1982; Jamieson 1969, 1976; Kellman 2003; Koch 1950a; Lawton

1966, 1971; McGrew 1976; Showers 1982; Yurky 1990, 1995. As *Hypnum bestii* Williams 1901. As *Limnobia bestii* Holzinger 1901.

Illustrations: Czernyadjera 2000; Flowers 1973; Ireland 1982; Jamieson 1976; Lawton 1966, 1971.

Geographic subdivisions: CaR, CW, MP, NW, SN, SNE.

Selected specimens: Del Norte Co.: Knopti Creek Road about 9 miles east of Highway 199, *Norris* 7754 (determined by Jamieson); Inyo Co.: Taboose Creek Trail, John Muir Wilderness, Inyo National Forest, *Shevock* 13880; Lake Co.: Big Spring, Boggs Mountain State Forest, *Toren & Dearing* 7108 (CAS); Modoc Co.: Soup Creek Campground east of Likely, Modoc National Forest, *Norris* 9450 (determined by Jamieson); Plumas Co.: Domingo Springs about 8 air miles northwest of Chester, Lassen National Forest, *Shevock & Corbin* 12233; Riverside Co.: Devils Slide Trail, San Jacinto Wilderness, San Bernardino National Forest, *Shevock, Kramer, Hall, & Ward* 24061; Santa Cruz Co.: Castle Rock Falls, Castle Rock State Park, *Kellman* 2259 (CAS); Siskiyou Co.: trail between Abbott Ranch and English Lake, Marble Mountain Wilderness, Klamath National Forest, *Spjut* 1358 (UC) [determined by Jamieson].

****Hygrohypnum cochlearifolium* (Venturi in De Notaris) Brotherus** [Campyliaceae]

Illustrations: As *Hygrohypnum smithii* var. *goulardii* Lawton 1971.

Geographic subdivisions: SN, SNE.

Selected specimens: Inyo Co.: Dragon Peak and north of Golden Trout Lake near Onion Valley, Inyo National Forest, *Norris* 46746; Madera Co.: Rock Creek about 0.4 mile south of Rock Creek Bridge, Sierra National Forest, *Norris & Shevock* 100023.

***Hygrohypnum duriusculum* (De Notaris) Jamieson** [Campyliaceae]

Literature: Jamieson 1976. As *Hygrohypnum dilatatum* Holmberg 1969; Koch 1950a; Spjut 1971.

Illustrations: Ireland 1982; Jamieson 1976; Koponen et al. 1995; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Fresno Co.: Grizzly Falls adjacent to the South Fork Kings River, Sequoia National Forest, *Shevock* 12446; Inyo Co.: slopes east of Dragon Peak north of Golden Trout Lake near Onion Valley, John Muir Wilderness, Inyo National Forest, *Norris* 46714; Siskiyou Co.: Horsetail Falls along road from Seiad Valley to Cook and Green Pass north of Seiad Valley, *Norris* 57622 and Paynes Creek, Klamath National Forest, *Norris* 46288.

***Hygrohypnum luridum* (Hedwig) Jennings** [Campyliaceae]

Literature: Flowers 1973; Harpel 1980a; Jamieson 1976; Koch 1950a, 1958; Lawton 1971; Showers 1982; Spjut 1971. As *Hypnum pseudo-arcticum* Howe 1897. As *Limnobia palustre* Howe 1896.

Illustrations: Abramov and Volkova 1998; Flowers 1973; Hedenäs 2003; Ireland 1982; Jamieson 1976; Kanda 1978; Koponen et al. 1995; Lawton 1971; Smith 1978.

Geographic subdivisions: NW, SN, SNE.

Selected specimens: Inyo Co.: above Golden Trout Lake northwest of Onion Valley, John Muir Wilderness, Inyo National Forest, *Norris* 46709; Mono Co.: Mildred Lake above Convict Lake, Inyo National Forest, *Norris* 71413; Tehama Co.: Anthony Peak, Mendocino National Forest, *Norris* 55044; Tulare Co.: above Primrose Lake, Sequoia National Park, *J.T. Howell s.n.* (CAS); Tuolumne Co.: Highway 108 about 1.5 miles below Sonora Pass, Stanislaus National Forest, *Norris* 78837.

***Hygrohypnum molle* (Hedwig) Loeske** [Campyliaceae]

Literature: Flowers 1973; Frantz and Cordone 1967; Harpel 1980a; Harthill et al. 1979; Jamieson 1976; Koch 1950a, 1958; McGrew 1976; Showers 1982; Spjut 1971; Strid 1974; Toren 1977.

Illustrations: Flowers 1973; Jamieson 1976; Lawton 1971.

Geographic subdivisions: CaR, SN, SW.

Selected specimens: El Dorado Co.: Round Lake, Eldorado National Forest, *Norris* 71162; Fresno Co.: Taboose Pass Trail, headwaters of the South Fork Kings River, Kings Canyon National Park, *Shevock* 13867; Placer Co.: canyon feeding Ward Creek near junction with Courchevel Road, *Whitemore* 3075 (MO); Plumas Co.: stream near Johnsville, *Ikenberry* 371 (MO); Riverside Co.: North Fork San Jacinto River, San Jacinto State Park, *Harpel* 1122 (pers. herb.) [confirmed by Schofield]; Tulare Co.: Kern Plateau, Sirretta Creek above Big Meadow, Sequoia National Forest, *Shevock* 17511 and trail between Silliman Pass and Lodgepole, Sequoia National Park, *Norris* 46516; Tuolumne Co.: Deadman Creek off of Highway 108 west of Sonora Pass, Stanislaus National Forest, *Shevock* 18599 (determined by Ochyra).

***Hygrohypnum ochraceum* (Turner ex Wilson) Loeske** [Campyliaceae]

Literature: Flowers 1973; Ireland 1982; Jamieson 1976; Koch 1950a, 1958; Koch and Ikenberry 1954; Lawton 1971; McGrew 1976; Spjut 1971. As *Hypnum ochraceum* Coville 1893.

Illustrations: Flowers 1973; Ireland 1982; Jamieson 1976; Kanda 1978; Koponen et al. 1995; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Calaveras Co.: south of Lake Alpine, 5.4 miles from county line on Highway 4, Stanislaus National Forest, *Mueller* 6699 (UC); Inyo Co.: above Chocolate Lake west of Big Pine, John Muir Wilderness, Inyo National Forest, *Norris* 46926; Nevada Co.: area of Donner Lake along stream, Tahoe National Forest, *Whitemore* 3053 (MO); Siskiyou Co.: Sugar Lake west of Callahan, Klamath National Forest, *Norris* 57387; Trinity

Co.: tributary of Coffee Creek near South Fork, *Norris 9361* (determined by Jamieson); Tulare Co.: trail east of Mitchell Peak toward Mitchell Meadow, Kings Canyon National Park, *Shevock 14562*.

***Hygrohypnum smithii* (Swartz in Liljeblad)**

Brotherus [Campylaceae]

Literature: Flowers 1973; Jamieson 1976; Koch 1950a, 1958; Koch and Ikenberry 1954; Lawton 1971; McGrew 1976; Showers 1982. As *Hypnum arcticum* Lesquereux 1868; Watson 1880.

Illustrations: Abramov and Volkova 1998; Flowers 1973; Jamieson 1976; Lawton 1971.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Fresno Co.: Forest Road 9S10 at tributary of Cow Creek, Sierra National Forest, *Shevock 14207*; Inyo Co.: Bighorn Sheep Zoological Area, Baxter Pass Trail, John Muir Wilderness, Inyo National Forest, *Shevock & York 16545*; Plumas Co.: stream near Quincy, *Ikenberry 1322* (MO) [determined by Koch]; Shasta Co.: Drakesbad, Warner Valley, Lassen Volcanic National Park, *Showers 2427* (UC); Siskiyou Co.: Sugar Lake west of Callahan, Klamath National Forest, *Norris 57380* and Paynes Lake, *Norris & Smith 46359*.

***Hygrohypnum styriacum* (Limpricht) Brotherus**

[Campylaceae]

Literature: Jamieson 1976.

Illustrations: Jamieson 1976.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Fresno Co.: Mist Falls Trail near junction of Bubbs Creek, Kings Canyon National Park, *Shevock & York 14469*; Inyo Co.: east of Dragon Peak and north of Golden Trout Lake near Onion Valley, John Muir Wilderness, Inyo National Forest, *Norris 46717*; Mono Co.: Highway 120 below Ellery Lake east of Tioga Pass, Inyo National Forest, *Shevock 13784* (determined by Jamieson) and Koenig Lake near Leavitt Lake east of Sonora Pass, Toiyabe National Forest, *Norris 57177*; Trinity Co.: Bullards Basin, Shasta-Trinity National Forest, *Norris 9287*.

***Hylocomium splendens* (Hedwig) Bruch & W.**

P. Schimper [Hylocomiaceae]

Literature: Holmberg 1969; Koch 1950a; Lawton 1971.

Illustrations: Buck 1998; Crum and Anderson 1981; Ignatov et al. 1996; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: about 2 miles west of Gasquet, Six Rivers National Forest, *Norris 7820* (determined by Rohrer) and South Fork Smith River near Rock Creek Ranch about 8 miles from Hiouchi, Six Rivers National Forest, *Dillingham 868* (CAS, UC); Siskiyou Co.: Middle Fork Applegate Trail near French Gulch, Rogue River National Forest, *Rolle & Rolle s.n.* (CAS, UC).

***Hymenostylium recurvirostre* (Hedwig) Dixon**

[Pottiaceae]

Literature: Zander 1977a. As *Gymnostomum recurvirostre* Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Long 1978; Mishler 1978.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978; Zander 1993.

Geographic subdivisions: CaR, DMoj, SN, SNE, SW.

Selected specimens: Inyo Co.: Main Fork Trail Canyon, base of Wilrose Peak, Death Valley National Park, *Shevock, York, Glazer, & Laeger 21853*; Kern Co.: Pine Tree Canyon west of Barren Ridge, *Shevock, Ertter, & Hare 17836*; Los Angeles Co.: Pacoima Dam, San Fernando Valley, *MacFadden 8171* (MO) [determined by Bartram]; Mono Co.: Convict Lake Trail between Convict Lake and Lake Mildred, Inyo National Forest, *Whittemore 1541a* (CAS) and *Norris 71372*; Shasta Co.: Upper Manzanita Creek at base of Crescent Cliffs, Lassen Volcanic National Park, *Showers 3924a* (UC); Tulare Co.: Limestone Cliffs, Kern River Canyon along County Road M-99, Sequoia National Forest, *Shevock 17062*.

***Hypnum circinale* W. J. Hooker** [Hypnaceae]

Literature: Bourell 1981; Holmberg 1969; Howe 1897; Jamieson 1969; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Smith 1970; Spjut 1971; Thomson and Ketchledge 1958; Toren 1977; Watson 1880; Yurky 1990, 1995.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, CW, NW.

Selected specimens: Butte Co.: Brush Creek, Plumas National Forest, *Dillingham 856* (CAS); Del Norte Co.: Highway 199 along Smith River about 9 miles east of junction with Highway 101, *Norris 85019*; Lake Co.: Summit Lake east of Mt. Sanhedrin, Mendocino National Forest, *Toren & Dearing 7202* (CAS); Marin Co.: Muir Woods National Monument, *Hermann 17496* (CAS); Mendocino Co.: Fox Creek north of Branscomb, The Nature Conservancy Branscomb Reserve, *Norris 47117*; Plumas Co.: below Cresta Power Station, *Norris 52645*; Santa Cruz Co.: Sempervirens Creek near Camp 7, Big Basin Redwood State Park, *Koch 2030a* (UC) and Opal Creek, *Kellman 1015* (CAS); Siskiyou Co.: between Wilderness Falls and Doe Flat, Klamath National Forest, *Norris 67806*.

***Hypnum dieckii* Renauld & Cardot** [Hypnaceae]

Literature: Holmberg 1969.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Del Norte Co.: near Prescott Cabin, *Norris 9023*; Humboldt Co.: Mill Creek, Forest Road 10N02, Six Rivers National Forest,

Norris 70604; Siskiyou Co.: Sugar Creek at Sugar Lake west of Callahan, Klamath National Forest, *Norris 57307*; Trinity Co.: Ditch Gulch below Highway 3 about 1 mile north of Highway 36, *Norris 68685*; Tulare Co.: East Fork Kaweah River below Atwell Mills Campground, Sequoia National Park, *Norris 46460*.

****Hypnum lindbergii* Mitten** [Hypnaceae]

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981.

Geographic subdivisions: SN.

Selected specimens: Nevada Co.: Boreal Ski Area, Tahoe National Forest, *Norris 102658*.

***Hypnum revolutum* (Mitten) Lindberg**
[Hypnaceae]

Literature: Koch 1950a, 1958; Lawton 1971; Showers 1982.

Illustrations: Flowers 1973; Ignatov et al. 1996; Lawton 1971; Ochyra 1998a; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: DMOj, NW, SN, SNE, SW.

Selected specimens: Del Norte Co.: Bear Basin Creek north of Bear Basin Butte, *Norris 68894*; El Dorado Co.: Silver Creek at Rat Castle Campground, *Norris 58553*; Inyo Co.: slopes above Chocolate Lake west of Big Pine, John Muir Wilderness, Inyo National Forest, *Norris 46910* and Sabrina Basin, Inyo National Forest, *Shevock 15332*; San Bernardino Co.: Curtis Canyon, Clark Mountain Wilderness, Mojave National Preserve, Mojave Desert, *Shevock, Spence, Glazer, & Laeger 23675*; Tulare Co.: Middle Fork Kaweah River at Little Deer Creek off of Crystal Cave Road, Sequoia National Park, *Shevock & Tseng 15776*.

***Hypnum subimponens* Lesquereux** [Hypnaceae]

Literature: Bourell 1981; Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Spjut 1971; Toren 1977; Watson 1880; Yurky 1990, 1995.

Illustrations: Lawton 1971.

Geographic subdivisions: CW, NW, SN.

Selected specimens: Marin Co.: Samuel P. Taylor Park, *Wagner s.n.* (UC); Mendocino Co.: Eel River about 3 miles south of Piercy, *Norris 72143*; Placer Co.: road to Bowman Lake about 2 miles north of Highway 20, *Norris 77021*; Santa Cruz Co.: South Fork Fall Creek, Henry Cowell Redwoods State Park, *Kellman 358* (CAS); Siskiyou Co.: west branch of Sutcliffe Creek about 13 miles northwest of Happy Camp, Klamath National Forest, *Norris 83299*; Tulare Co.: Crystal Cave Road at junction with Little Deer Creek, Sequoia National Park, *Shevock 15642*.

****Hypnum vaucheri* Lesquereux** [Hypnaceae]

Illustrations: Flowers 1973; Ignatov et al. 1996; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: SNE.

Selected specimens: Inyo Co.: Methuselah Trail in Schulman Grove, Ancient Bristlecone Pine Forest Botanical Area, White Mountains, Inyo National Forest, *Norris 99518*.

***Isopterygiopsis pulchella* (Hedwig) Iwatsuki**
[Hypnaceae]

Literature: As *Isopterygium pulchellum* Harpel 1980a; Ireland 1982; Koch 1950a; Lawton 1971; Showers 1982; Spjut 1971.

Illustrations: Ignatov et al. 1996; Ireland 1982; Lawton 1971; Smith 1968.

Geographic subdivisions: NW, SN, SW.

Selected specimens: Fresno Co.: Lockwood Redwood Grove, Sequoia National Forest, *Norris, Shevock, & York 87916*; Riverside Co.: Wellmans Cienega, San Jacinto Mountains, San Jacinto State Park, *Harpel 951* (pers. herb.); Siskiyou Co.: Terrace and Upper Cliff Lakes, *Norris 53036* and Sawtooth Ridge at crest of Caribou Rim along trail from Big Flat to Caribou Basin, *Norris 9213*; Tulare Co.: Lower Soldier Lake, Sequoia National Park, *J.T. Howell s.n.* (CAS) and north slope Slate Mountain, Sequoia National Forest, *Shevock 15670*; Tuolumne Co.: Pilot Ridge, Stanislaus National Forest, *Shevock 13268*.

****Isopterygium tenerum* (Swartz) Mitten**
[Hypnaceae]

Illustrations: Buck 1998; Ireland 1982; Iwatsuki and Crosby 1979; Sharp et al. 1994.

Geographic subdivisions: SN.

Selected specimens: El Dorado Co.: Ropi Lake, Desolation Wilderness, Eldorado National Forest, *Norris 71114*.

****Isothecium cardotii* Kindberg**
[Brachytheciaceae]

Illustrations: No illustration located for this species.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: El Dorado Co.: Bear Creek Picnic Area near Georgetown, *Norris & Piippo 82337*; Humboldt Co.: about 1 mile north of Indianola, *Norris 10260* and Forest Road 10N02 at head of Mill Creek, Six Rivers National Forest, *Norris 70571*; Shasta Co.: Forest Road 39N07 along Soda Creek about 6 miles northeast of Interstate 5 south of Dunsuir, *Norris & Hillyard 103834*; Siskiyou Co.: South Fork Salmon River near junction with West Fork, *Norris 10088*; Tuolumne Co.: Pilot Ridge, Stanislaus National Forest, *Shevock 13267 & 13277*.

***Isothecium cristatum* (Hampe) H. Robinson**
[Brachytheciaceae]

Literature: Bourell 1981; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Lawton 1971; McCleary 1972; Shevock and Toren 2001; Smith 1970; Toren 1977; Yurky 1990, 1995. As *Bestia cristata* Koch 1950a, 1951e; Koch and Ikenberry

1954. As *Bestia breweriana* Steere 1954; Thomson and Ketchledge 1958. As *Hypnum brewerianum* Brandegee 1891; Koch 1950a; Lesquereux 1868. As *Hypnum aggregatum* Lesquereux 1868; Watson 1880. As *Isothecium brewerianum* Bradshaw 1926; Howe 1897; Kingman 1912. As *Isothecium howei* Howe 1896.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: El Dorado Co.: Highway 50 along South Fork American River at Bridal Veil Falls Campground, *Norris* 58420; Humboldt Co.: Emerald Creek at junction with Redwood Creek, Redwood National Park, *Norris* 45827; Marin Co.: trail near Mud Lake, Point Reyes National Seashore, *Norris* 71842; San Francisco Co.: Glen Canyon, San Miguel Hills, *Shevock* 18875 & 18891; Santa Cruz Co.: Highway 9 about 1.5 miles north of Boulder Creek, *Norris* 55596; Shasta Co.: Brandy Creek Picnic Area, Whiskeytown National Recreation Area, *Norris* 73619; Sonoma Co.: Green Valley Creek about 0.25 mile south of Highway 116, west of Forestville, *Norris* 101115.

***Isothecium myosuroides* Bridel**

[Brachytheciaceae]

Literature: Allen 1983; Holmberg 1969; Jamieson 1969; Kellman 2003; McGrew 1976; Shevock and Toren 2001; Smith 1970; Whittemore and Sommers 1999; Yurky 1995. As *Hypnum myosuroides* Brandegee 1891; Lesquereux 1868; Sullivant 1856; Watson 1880.

Illustrations: Smith 1978.

Geographic subdivisions: CW, NW, SN.

Selected specimens: San Benito Co.: trail to the caves, Pinnacles National Monument, *Koch* 1325a (UC); Santa Cruz Co.: near Stevens Redwood Grove, *Schofield* 8328 (UC); Trinity Co.: East Fork Road at Rich Gulch, north of Helena, Shasta-Trinity National Forest, *Norris* 18950; Tulare Co.: tributary of Squirrel Creek, Sequoia National Park, *Norris*, *Shevock*, & *Barahona* 87550.

***Isothecium obtusatum* Kindberg**

[Brachytheciaceae]

Literature: Kellman 2003.

Illustrations: Allen and Whittemore 1996.

Geographic subdivisions: CW, NW.

Selected specimens: Del Norte Co.: exit of Sanger Lake along Forest Road 4803 southeast of O'Brien, Six Rivers National Forest, *Norris* 70834; Marin Co.: trail to Mud Lake, Point Reyes National Seashore, *Norris* 71813; Placer Co.: Highway 49 about 1 mile south of Forest Hill Road, *Whittemore* 3541 (CAS); San Mateo Co.: between headquarters and Tiptoe Falls, Portola State Park, *Whittemore* 4112 (CAS); Santa Cruz Co.: San Lorenzo River near the Saratoga Toll Road about 7 miles north of Boulder Creek off Highway 9, *Kellman* 2535 (CAS).

***Isothecium spiculiferum* (Mitten) Renauld & Cardot** [Brachytheciaceae]

Literature: Bourell 1981; Harthill et al. 1979; Shevock and Toren 2001; Showers 1982; Toren 1977.

Illustrations: No illustration located.

Geographic subdivisions: CW, NW.

Specimens examined: Del Norte Co.: Coastal Trail between False Klamath Cove and Requa, Redwood National and State Parks, *Norris* 70361; Humboldt Co.: Chemise Mountain Trail from Nadelos Recreation Site, BLM Kings Range Conservation Area, *Norris* 67713; San Francisco Co.: Mt. Sutro, *Shevock* 19181 and Golden Gate Park, *Shevock* 19204.

***Isothecium stoloniferum* Bridel**

[Brachytheciaceae]

Literature: Holmberg 1969; Lesquereux 1868; Spjut 1971; Yurky 1990. As *Pseudoisothecium stoloniferum* Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Thomson and Ketchledge 1958.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: El Dorado Co.: South Fork American River at Carpenter Creek, *Norris* 58439 and Whaler Creek south of Quintette, *Norris* & *Piippo* 82360; Humboldt Co.: about 3 miles north of Avenue of the Giants, *Norris* 72148; Mendocino Co.: Mill Creek, *Norris* 53256; Shasta Co.: Shotgun Creek near North Fork Shotgun Creek southeast of Sims, *Norris* & *Hillyard* 103869; Sonoma Co.: Sonoma, *Bioletti s.n.* (UC).

***Jaffueliobryum raui* (Austin) Thériot**

[Grimmiaceae]

Literature: Harpel 2000. [See Churchill 1987 for description and distribution.]

Illustrations: Churchill 1987. As *Grimmia rauii* Crum and Anderson 1981; Flowers 1973.

Geographic subdivisions: DMoj, SN, SNE, SW.

Selected specimens: Riverside Co.: Bull Canyon Road, San Jacinto Mountains, San Bernardino National Forest, *Harpel* 1177 (UBC, UC) [confirmed by Schofield] and Martinez Canyon near Aqua Alta Canyon, Santa Rosa Mountains, Colorado Desert, *Wheeler* 8813 (CAS, UC); Tulare Co.: Forks of the Kern River, Golden Trout Wilderness, Sequoia National Forest, *Shevock* 16526.

****Jaffueliobryum wrightii* Sullivant in Sullivant & Lesquereux** [Grimmiaceae]

Illustrations: Churchill 1987. As *Grimmia wrightii* Crum and Anderson 1981; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: DMoj, SNE.

Selected specimens: Inyo Co.: Grandview Campground near Grandview Mine, White Mountains, Inyo National Forest, *Wheeler* 8511 (CAS, UC); San Bernardino Co.: Coyote Canyon, Granite Mountains, north of Highway 40, Mojave National Preserve, *Norris* 87856.

Kiaeria blyttii* (Bruch & W. P. Schimper)*Brotherus** [Dicranaceae]**Literature:** Crum and Anderson 1981; Showers 1982.**Illustrations:** Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982. As *Arctoa blyttii* Lawton 1971.**Geographic subdivisions:** CaR, NW.**Selected specimens:** Shasta Co.: boulder slope west of Lost Creek Camp, Lassen Volcanic National Park, *Showers* 3738 (UC); Siskiyou Co.: Gulch Lake southwest of Callahan, Klamath National Forest, *Norris* 57531 and Granite Creek between Tickner Creek and Blue Granite Lake, *Norris* 52312; Trinity Co.: rivulet below East Weaver Lake, *Norris* 9406 and near Browns Meadows, *Norris* 23143.***Kiaeria falcata* (Hedwig) I. Hagen** [Dicranaceae]**Literature:** McGrew 1976.**Illustrations:** Smith 1978. As *Arctoa falcata* Lawton 1971.**Geographic subdivisions:** CaR, NW.**Selected specimens:** Siskiyou Co.: above confluence of drainages from Lower Russian and Golden Russian Lakes, Klamath National Forest, *McGrew* 360 (UC), near Paynes Lake, Klamath National Forest, *Norris & Smith* 46354 & 46376; Granite Creek between Tickner Creek and Granite Lake, *Norris* 52309, and eastern slopes of Little Grayback, *Holmberg* 942 (UC).***Kiaeria starkei* (Weber & D. Mohr) I. Hagen**

[Dicranaceae]

Literature: McGrew 1976.**Illustrations:** Crum and Anderson 1981; Ireland 1982; Smith 1978. As *Actoa starkei* Lawton 1971.**Geographic subdivisions:** CaR, NW, SN, SNE.**Selected specimens:** Del Norte Co.: slopes above Whiskey Lake, Siskiyou National Forest, *Norris* 57691 & 57713; Humboldt Co.: headwaters of Oregon Creek north of Trinity Summit Guard Station, *Norris & Creek* 50104; Inyo Co.: slopes above Treasure Lake west of Big Pine, John Muir Wilderness, Inyo National Forest, *Norris* 46941; Siskiyou Co.: trail to Long Gulch Lake southwest of Callahan, Klamath National Forest, *Norris* 57520; Trinity Co.: trail to Long Gulch Lake, Klamath National Forest, *Spjut, Norris, & J. Koponen* 6296 (UC).***Kindbergia oregana* (Sullivant) Ochyra**

[Brachytheciaceae]

Literature: Shevock and Toren 2001; Yurky 1990. As *Eurhynchium brittoniae* Koch 1950a; Lawton 1971. As *Eurhynchium oreganum* Holmberg 1969; Howe 1897; Jamieson 1969; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Smith 1970; Spjut 1971; Thomson and Ketchledge 1958; Yurky 1995. As *Hypnum oreganum* Lesquereux 1868; Sullivant 1856; Watson 1880. As *Stokesiella oregana* Bourell 1981; McGrew 1976; Toren 1977.**Illustrations:** Lawton 1971.**Geographic subdivisions:** CaR, CW, MP, NW, SN, SW.**Selected specimens:** Monterey Co.: Salmon Creek Trail, Santa Lucia Mountains, Los Padres National Forest, *Norris* 68223; San Francisco Co.: Mt. Davidson, *Shevock* 18923; Santa Barbara Co.: Windmill Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock* 20901; Shasta Co.: Highway 299 on north side of Haynes Flat about 3 miles west of Burney, *Norris* 68454; Siskiyou Co.: west of White Mountain near Cook and Green Pass, Klamath National Forest, *Norris* 50185; Sonoma Co.: Gualala River near Lee Noble Road, *Norris* 86977; Tulare Co.: Freeman Creek Grove, Lloyd Meadows Basin, Sequoia National Forest, *Shevock* 3890.***Kindbergia praelonga* (Hedwig) Ochyra**

[Brachytheciaceae]

Literature: Shevock and Toren 2001; Yurky 1990. As *Eurhynchium praelongum* Kellman 2003; Kingman 1912; Koch 1950a; McCleary 1972; Smith 1970; Spjut 1971; Stark and Whittemore 1992; Whittemore and Sommers 1999; Yurky 1995. As *Eurhynchium praelongum* var. *stokesii* Holmberg 1969; Lawton 1971; McCleary 1972. As *Eurhynchium stokesii* Jamieson 1969; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Spjut 1971. As *Hypnum stokesii* Lesquereux 1868; Watson 1880. As *Stokesiella praelonga* Bourell 1981; Harthill et al. 1979; Ireland 1982; Long 1978; Showers 1982; Toren 1977.**Illustrations:** Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978.**Geographic subdivisions:** CaR, CW, MP, NW, SN, SNE, SW.**Selected specimens:** Fresno Co.: Deer Cove Creek along Highway 180, South Fork Kings River, Sequoia National Forest, *Shevock* 12456; Humboldt Co.: Prairie Creek Redwood State Park, *Norris* 7940; Monterey Co.: Mill Creek Picnic Area, *Norris* 48571; Placer Co.: road to Bowman Lake about 2 miles north of Highway 20, *Norris* 77002; San Francisco Co.: Mt. Davidson, *Shevock* 18925; Santa Barbara Co.: Lobos Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock & Rodriguez* 20848; Shasta Co.: Shasta Lake at Interstate 5 near Bridge Mountain Road, Shasta-Trinity National Forest, *Norris* 72906.***Leptobryum pyriforme* (Hedwig) Wilson**

[Meesiaceae]

Literature: Cooke 1941; Coville 1893; Crum and Anderson 1981; Harpel 1980a; Harthill et al. 1979; Kellman 2003; Kingman 1912; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Long 1978; McGrew 1976; Mishler 1978; Shevock and Toren 2001; Showers 1982; Strid 1974; Toren 1977; Watson 1880. As *Bryum pyriforme* Lesquereux 1868; Sullivant 1856.**Illustrations:** Abramov and Volkova 1998; Allen

2002; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, DMoj, DSon, MP, NW, SN, SNE, SW.

Selected specimens: Inyo Co.: South Lake Road, 0.7 mile below South Lake, Inyo National Forest, *Shevock 12538* and Humingbird Spring near Rogers Peak, Death Valley National Park, *Shevock, York, and Davis 21374*; Lake Co.: west base of Goat Mountain near Addington Springs, Mendocino National Forest, *Toren & Dearing 7551* (CAS); Madera Co.: San Joaquin River below Red Creek, Devils Postpile National Monument, *Shevock & Dulen 21271*; Modoc Co.: near Post Canyon north of Adin, *Norris 47403*; Mono Co.: O'Harrel Canyon northeast of Lake Crowley, Glass Mountain, Inyo National Forest, *Shevock & York 19994*; Monterey Co.: near Wagon Caves Campground, Los Padres National Forest, *Norris 48551*; Riverside Co.: Forty Nine Palms Oasis near Twenty Nine Palms, *Norris 58025*; San Francisco Co.: Presidio of San Francisco, *Shevock 19366*; Siskiyou Co.: near Bear Lake, Klamath National Forest, *Norris 24197*.

***Leptodictyum humile* (Palisot de Beauvois)**

Ochyra [Amblystegiaceae]

Literature: As *Amblystegium trichopodium* Lawton 1971. As *Leptodictyum trichopodium* Harthill et al. 1979; Holmberg 1969; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Mishler 1978; Showers 1982; Strid 1974; Toren 1977.

Illustrations: Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, DMoj, NW, SN, SNE, SW.

Selected specimens: Fresno Co.: Kearsarge Lakes, Kings Canyon National Park, *Shevock 14333*; Inyo Co.: Johnson Canyon, Panamint Mountains, Death Valley National Park, *Shevock, Harpel, & York 19075*; Mariposa Co.: Crane Flat Meadow, Yosemite National Park, *Kellman 549* (CAS); Placer Co.: Highway 89, west shore of Lake Tahoe, USFS Lake Tahoe Management Unit, *Koch 1958* (UC); Tehama Co.: Tomhead Gulch, Shasta-Trinity National Forest, *Norris 56902*; Tulare Co.: shore of Oriole Lake, Sequoia National Park, *Norris, Shevock, & Barahona 87533*; Tuolumne Co.: Highway 108 at Frazier Flat Campground, Stanislaus National Forest, *Spjut, Norris, & J. Koponen 6253* (UC).

***Leptodictyum riparium* (Hedwig) Warnstorf**

[Amblystegiaceae]

Literature: Frantz and Cordone 1967; Harthill et al. 1979; Kellman 2003; Koch 1950a, 1958; Koch and Ikenberry 1954; McGrew 1976; Mishler 1978; Shevock and Toren 2001; Showers 1982; Strid 1974; Toren 1977; Yurky 1990, 1995. As *Amblystegium riparium* Kingman 1912; Lawton 1971; Spjut 1971. As *Hypnum riparium* Lesquereux 1868; Sullivant 1856; Watson 1880.

Illustrations: Buck 1998; Hedenäs 2003; Ireland

1982; Koponen et al. 1995; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN, SNE, SW.

Selected specimens: Fresno Co.: below West Lake near Sand Flat, Sierra National Forest, *Shevock 14189*; Cedar Grove, Zumwalt Meadows along the South Fork Kings River, Kings Canyon National Park, *Shevock 13730*; Mendocino Co.: near Howard Lake, Mendocino National Forest, *Shevock & Isle 15903*; Mono Co.: Mormon Meadow along Highway 270, Bodie Hills, *Shevock 15246*; San Benito Co.: Pinnacles National Monument, *Blasdale s.n.* (UC); San Francisco Co.: Alamo Square, *Shevock 18909*; Shasta Co.: Bumpass Hell, Lassen Volcanic National Park, *Showers 861* (UC); Tulare Co.: Oriole Lake, Sequoia National Park, *Shevock 17619* (determined by Ochrya).

***Leptophascum leptophyllum* (C. Müller Hal.) J.**

Guerra & M. J. Cano [Pottiaceae]

Literature: As *Chenia leptophylla* Kellman 2003; Shevock and Toren 2001.

Illustrations: Arts and Sollman 1991; Guerra and Cano 2000; Guerra and Cros 2003. As *Chenia leptophylla* Zander 1993.

Geographic subdivisions: CW, GV.

Selected specimens: Merced Co.: banks of road about 0.5 mile east of Snelling along Merced River, *Norris 69844*; San Francisco Co.: Lincoln Blvd and 41st Street, Golden Gate Park, *Toren 2921* (CAS, SFSU); Santa Cruz Co.: Liddell Creek Fire Road at Highway 1 south of Davenport, *Kellman 755* (CAS, UC).

****Leptopterigynandrum austro-alpinum* C. Müller Hal.** [Leskeaceae]

Illustrations: Sharp et al. 1994.

Geographic subdivisions: DMoj.

Selected specimens: San Bernardino Co.: Kingston Peak, Kingston BLM Wilderness, Mojave Desert, *Laeger & Bogan 1759* (CAS).

****Lescuraea atricha* (Kindberg) Latwon**

[Leskeaceae]

Illustrations: Lawton 1957, 1971.

Geographic subdivisions: CaR.

Selected specimens: Siskiyou Co.: McCloud River Preserve, The Nature Conservancy, *Norris & Hill-yard 106544*.

***Lescuraea incurvata* (Hedwig) E. Lawton**

[Leskeaceae]

Literature: McGrew 1976; Spjut 1971. As *Lescuraea incurvata* var. *gigantea* Spjut 1971. As *Lescuraea incurvata* var. *tenuiretis* Spjut 1971.

Illustrations: Flowers 1973; Lawton 1957, 1971; Noguchi 1972; Smith 1978.

Geographic subdivisions: CaR, MP, NW, SN.

Selected specimens: Amador Co.: Caples Creek north of Kirkwood Lake, Eldorado National Forest, *Norris 82746*; Modoc Co.: Alcohol Crater Rim,

Modoc National Forest, *Harpel* 16329 (pers. herb.); Siskiyou Co.: near Taylor Lake, Klamath National Forest, *Norris* 83397 (confirmed by Krieger) and Clear Creek Trailhead, southeast slope of Mt. Shasta, Shasta-Trinity National Forest, *Norris & Hillyard* 104063 and Shackleford Creek Trail, Marble Mountain Wilderness, Klamath National Forest, *Norris & Hillyard* 104989; Tehama Co.: Battle Creek along Forest Road 29N35 about 4 miles east of Mineral, Lassen National Forest, *Norris* 48163 (confirmed by Krieger); Trinity Co.: Canyon Creek between Ripstein Camp and McKay Camp, *Norris* 8024 (confirmed by Krieger); Tulare Co.: along Forest Road 13S45 at tributary of Bearskin Creek, Sequoia National Forest, *Shevock & York* 13682.

****Lescuraea pallida* (Best) Norris & Shevock**
comb nov. [Leskeaceae]

Lescuraea radicata (Mitten) Mönkemeyer var. *pallida* (Best) E. Lawton. Bulletin Torrey Botanical Club 84:306. 1957. *Pseudoleskea radicata* (Mitten) Macoun & Kindberg var. *pallida* Best. Bulletin Torrey Botanical Club 27:227. 1900.

Illustrations: Lawton 1957, 1971.

Geographic subdivisions: SN, SNE.

Selected specimens: Alpine Co.: Red Lake Creek, Toiyabe National Forest, *Norris* 88130; Inyo Co.: slopes of Treasure Lake west of Big Pine, John Muir Wilderness, Inyo National Forest, *Norris* 46968 (confirmed by Krieger); Mono Co.: Tioga Junction Campground about 2.5 miles north of Tioga Pass, Inyo National Forest, *Norris* 48348; Tulare Co.: Clover Creek east of Wuksachi Lodge, Sequoia National Park, *Shevock* 18278; Tuolumne Co.: Lower Young Lake, Yosemite National Park, *Messick* 674 (UC).

***Lescuraea patens* (Lindberg) Arnell & C. E. O. Jensen** [Leskeaceae]

Literature: Flowers 1973; Holmberg 1969; Jessup 2000; Lawton 1957, 1971; McGrew 1976; Spjut 1971. As *Pseudoleskea atrovirens* Cooke 1941; Koch 1950a. As *Pseudoleskea patens* Harthill et al. 1979; Koch 1958; Showers 1982; Strid 1974; Toren 1977.

Illustrations: Flowers 1973; Ireland 1982; Lawton 1957, 1971.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Alpine Co.: Tamarack Lake, Toiyabe National Forest, *Norris* 82777; Fresno Co.: north-face of Spanish Mountain, John Muir Wilderness, Sierra National Forest, *Shevock & York* 12424 (confirmed by Krieger); Glenn Co.: slopes of Black Butte, Mendocino National Forest, *Norris* 47973; Humboldt Co.: Tish-Tang-a-Tang Creek near Grogans Hole, Six Rivers National Forest, *Norris* 47826; Lake Co.: headwaters Bear Creek, Snow Mountain Wilderness, Mendocino National Forest, *Toren & Dearing* 7481 (CAS); Siskiyou Co.: Upper Cliff Lakes, Shasta-Trinity National

Forest, *Norris* 53034 and South Fork Russian River above Etna-Sawyers Bar Road, *Norris* 11891.

***Lescuraea radicata* (Mitten) Mönkemeyer**
[Leskeaceae]

Literature: Flowers 1973; Lawton 1957, 1971; McGrew 1976; Spjut 1971. As *Pseudoleskea radicata* Harthill et al. 1979; Showers 1982.

Illustrations: Flowers 1973; Lawton 1957, 1971; Noguchi 1972.

Geographic subdivisions: CaR, MP, NW, SN.

Selected specimens: Del Norte Co.: Doctor Rock, Six Rivers National Forest, *Norris* 50319 (confirmed by Krieger); Humboldt Co.: headwaters of Oregon Creek north of Trinity Summit Guard Station, *Norris & Creek* 50101; Modoc Co.: Pine Creek Basin Trail, South Warner Wilderness, Modoc National Forest, *Harpel* 2232 (pers. herb.); Siskiyou Co.: Highway 49 about 7 miles east of Yuba Pass, *Lawton* 3151 (UC); Shasta Co.: Soda Creek Road about 3 miles NE of Interstate 5 near Dunsuir, Shasta-Trinity National Forest, *Norris* 84771 and Castle Lake at Castle Lake Creek, southwest of Mt. Shasta City, *Norris & Hillyard* 103842; Siskiyou Co.: Big Boulder Lake west of Carrville, *Norris & Streimann* 74803; Trinity Co.: Long Gulch Lake, Trinity Alps Wilderness, Klamath National Forest, *Spjut, Norris, & J. Koponen* 6290 (UC).

****Lescuraea saviana* (De Notaris) E. Lawton**
[Leskeaceae]

Illustrations: Lawton 1957, 1971.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Del Norte Co.: exit of Sanger Lake southeast of O'Brien, Six Rivers National Forest, *Norris* 70780; Shasta Co.: Forest Road 39N07 along Soda Creek about 6 miles northeast of Interstate 5 south of Dunsuir, Shasta-Trinity National Forest, *Norris & Hillyard* 103836; Siskiyou Co.: trail to English Lake, Klamath National Forest, *Spjut* 1473 (UC); Trinity Co.: Canyon Creek between Ripstein Camp and McKay Camp, *Norris* 8033; Tulare Co.: near the Ponderosa Resort, eastern base of Slate Mountain, Sequoia National Forest, *Shevock* 15656.

***Lescuraea stenophylla* (Renauld & Cardot) Lindberg** [Leskeaceae]

Literature: Holmberg 1969; Spjut 1971. As *Pseudoleskea rigescens* Howe 1896; Koch 1950a.

Illustrations: Lawton 1957, 1971.

Geographic subdivisions: CaR, MP, NW.

Selected specimens: Del Norte Co.: Bear Basin Creek north of Bear Basin Butte, *Norris* 68878 & 68882; Humboldt Co.: Long Ridge near headwaters of Bunch Grass Creek, Hoopa Valley Indian Reservation, *Norris* 47806; Modoc Co.: Big Valley Mountains, *Baker & Nutting* 43 (UC); Siskiyou Co.: west branch of Sutcliffe Creek about 13 miles northwest of Happy Camp, Klamath National Forest, *Norris* 83291 & 83298 and above Neals Camp,

Mt. Shasta, Shasta-Trinity National Forest, *Howe 115* (UC).

***Leskea polycarpa* Ehrhart ex Hedwig**
[Leskeaceae]

Literature: McGrew 1976.

Illustrations: Ireland 1982; Lawton 1971; Noguchi 1972; Smith 1978.

Geographic subdivisions: NW, SN.

Selected specimens: Alpine Co.: Pacific Creek at Pacific Valley Campground, Highway 4 east of Pacific Grade Summit, Stanislaus National Forest, *Norris 77201*; Del Norte Co.: Bear Basin Butte, *Norris 8093b*; Fresno Co.: east base Maxson Dome near Courtwright Reservoir, John Muir Wilderness, Sierra National Forest, *Shevock & York 17444*; Humboldt Co.: South Fork Mountain Road near Doe Spring about 7 air miles north of Mad River, Six Rivers National Forest, *Norris 84072*; Tulare Co.: Western Divide, Peppermint Creek, Sequoia National Forest, *Laeger 290* (CAS).

***Leucolepis acanthoneura* (Schwägrichen)**
Lindberg [Mniaceae]

Literature: Howe 1897; Yurky 1990, 1995. As *Leucolepis menziesii* Bourell 1981; Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Smith 1970; Spjut 1971; Steere et al. 1954; Thomson and Ketchledge 1958; Toren 1977. As *Mnium menziesii* Bradshaw 1926; Lesquereux 1868; Sullivant 1856; Watson 1880.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Calaveras Co.: Moran Creek about 1 mile north of Avery, Stanislaus National Forest, *Wagner Jr. 4360a* (UC); El Dorado Co.: Bear Creek Picnic Area south-southwest of Georgetown, Eldorado National Forest, *Norris & Piippo 82338*; Humboldt Co.: between Cal Barrel Road and Elk Grove Park Headquarters, Prairie Creek Redwoods State Park, *Shevock 16741*; Madera Co.: Minarets Road at Rock Creek, Sierra National Forest, *Shevock & Kellman 19772*; Nevada Co.: tributary of Washington Creek 4.2 miles from Highway 20, Tahoe National Forest, *Shevock & Toren 20742*; Santa Cruz Co.: near George's Campground, Forest of Nisene Marks State Park east of Aptos, Santa Cruz Mountains, *Whittemore 4038* (CAS); Siskiyou Co.: Elliott Creek near Seattle Bar, Rogue River National Forest, *Shevock & Toren 20083*; Trinity Co.: Highway 36 at Swift Creek, Shasta-Trinity National Forest, *Norris 56551*.

****Lorentziella imbricata* (Mitten) Brotherus**
[Gigaspemaceae]

Illustrations: Lawton 1953; Rushing and Snider 1980; Sharp et al. 1994.

Geographic subdivisions: SW.

Selected specimens: San Diego Co.: San Dieguito River Park, Bernardo Rancho, *D. Baltzo s.n.* (UC).

****Meesia longiseta* Hedwig** [Meesiaceae]

Illustrations: Abramov and Volkova 1998; Allen 2002; Crum and Anderson 1981; Ignatov and Ignatova 2003; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: CaR, SN.

Selected specimens: Nevada Co.: about 0.5 mile northeast of Bowman Lake, Tahoe National Forest, *Ahart 10609* (UC); Plumas Co.: Willow Lake northwest of Chester, Lassen National Forest, *Norris 96251*; Tuolumne Co.: about 2 miles east of Tuolumne Meadows toward Tioga Pass, Yosemite National Park, *Norris 100353*.

***Meesia triquetra* (H. Richter) Ångström**
[Meesiaceae]

Literature: Crum and Anderson 1981; Howe 1896; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Montagnes 1990.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, NW, SN, SW.

Selected specimens: Butte Co.: Chico Creek, *Austin 229* (UC); El Dorado Co.: Grass Lake, Highway 89 west of Luther Pass and south of Lake Tahoe, Eldorado National Forest, *Norris 71312 & 79049* and *Koch & Stebbins 2316* (UC); Fresno Co.: between House and Ahart Meadows, west of Wishon Reservoir, Sierra National Forest, *Shevock & Bourrell 14041* and west of Kaiser Pass, Kaiser Wilderness, Sierra National Forest, *Shevock 20989*; Humboldt Co.: near McClellan Mountain about 5 miles east of Bridgeville, *Norris 45819*; Lassen Co.: East of Humbug Pass, Plumas National Forest, *Shevock & Erter 19887*; Nevada Co.: Mason's Bog at Sagehen, Tahoe National Forest, *Toren 1438* (SFSU); Riverside Co.: Wellmans Cienega, San Jacinto Mountains, San Jacinto State Park, *Shevock, Kramer, Hall, & Ward 24069*; Sierra Co.: Secret Meadow east of Independence Lake, Tahoe National Forest, *Norris 99457*; Siskiyou Co.: Sisson near Mt. Shasta, *Howe 102* (UC); Tulare Co.: Log Meadow near Crescent Meadow, Giant Forest, Sequoia National Park, *Shevock 16678*.

***Meesia uliginosa* Hedwig** [Meesiaceae]

Literature: Crum and Anderson 1981; Howe 1896; Koch 1950a; Lawton 1971; Lesquereux 1868; Watson 1880.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Ochyra 1998a; Smith 1978.

Geographic subdivisions: CaR, SN, SW.

Selected specimens: Fresno Co.: between Wet Meadow and Spanish Lake, John Muir Wilderness, Sierra National Forest, *Shevock 14153*; Sierra Co.: Secret Meadow east of Independence Lake, Tahoe National Forest, *Norris 99466*; Riverside Co.: Wellmans Cienega, east side of Marion Mountain, San Jacinto State Park, *Wheeler 7901* (CAS, DUKE,

UC) [determined by Shaw]; Siskiyou Co.: Sisson near Mt. Shasta, *Howe 117* (UC); Tulare Co.: South Mountaineer Creek at Summit Trail, Golden Trout Wilderness, Sequoia National Forest, *Shevock 14245*; Unspecified county: *Bolander 90* (UC).

***Meiotrichum lyallii* (Mitten) G. L. S. Merrill**
[Polytrichaceae]

Literature: As *Oligotrichum lyallii* Watson 1880. As *Polytrichadelphus lyallii* Flowers 1973; Holmberg 1969; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Spjut 1971. As *Polytrichastrum lyallii* McGrew 1976. As *Polytrichum lyallii* Lesquereux 1868; Showers 1982; Toren 1977.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Glenn Co.: slopes of Black Butte, Mendocino National Forest, *Norris 47974*; Humboldt Co.: Oregon Creek north of Trinity Summit Guard Station, *Norris & Creek 50144*; Lake Co.: Cedar Camp, Snow Mountain Wilderness, Mendocino National Forest, *Toren & Dearing 7491* (CAS); Mariposa Co.: Glacier Point Road about 1.2 miles east of Bridalveil Campground, Yosemite Park, *Norris & Shevock 100330*; Plumas Co.: Gibsons ville Ridge, crest of Quincy-LaPorte Road, Plumas National Forest, *Norris 83162*; Siskiyou Co.: Jaynes Creek northwest of Klamath River, *Norris 48698*; Tulare Co.: Big Meadows Road, 0.2 mile east of Rabbit Meadow Road, Sequoia National Forest, *Shevock 10864*.

***Metaneckera menziesii* (Drummond) W. C. Steere** [Neckeraceae]

Literature: Bourell 1981; Holmberg 1969; Jamieson 1969; Kellman 2003; Showers 1982; Spjut 1971; Steere 1967; Toren 1977; Yurky 1990, 1995. As *Neckera menziesii* Flowers 1973; Lawton 1971; Lesquereux 1868; Watson 1880. As *Neckeradelphus menziesii* Koch 1950a, 1951e; Koch and Ikenberry 1954; Steere 1941; Thomson and Ketchledge 1958.

Illustrations: Flowers 1973; Lawton 1971.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: El Dorado Co.: Sly County Park, *Norris 58585*; Humboldt Co.: Redwood Creek near Orick, Redwood National Park, *Norris 22363*; Lake Co.: Cold Creek west of Low Gap between Sheetiron Mountain and Snow Mountain, Mendocino National Forest, *Shevock, Toren, & Dearing 18791*; Mariposa Co.: Highway 41 near Wawona Entrance Station, Yosemite National Park, *Shevock 21437*; Santa Cruz Co.: Laguna Creek, Wilder Ranch State Park, *Kellman 1862* (CAS); Shasta Co.: Fall Creek Road about 1 mile southeast of McCloud Bridge at Shasta Lake, Shasta-Trinity National Forest, *Norris 84858*; Sonoma Co.: Wolf Creek Road about 4 miles east of Gualala, *Norris 86962*; Tulare Co.: Lake Canyon about 0.5 mile below Oriole Lake, Sequoia National Park, *Shevock 17611*.

***Microbryum davallianum* (J. E. Smith in Drake) Zander** [Pottiaceae]

Literature: Kellman 2003. As *Pottia davalliana* Crum and Anderson 1981. As *Pottia minutula* Lesquereux 1868; Lesquereux and James 1884.

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Williams 1961.

Geographic subdivisions: CW.

Selected specimens: Alameda Co.: just below Little Yosemite, Canyon View Trail and Camp Ohlone Road, Sunsol Regional Wilderness, *Whittemore 5454* (MO); Monterey Co.: Sam Jones Road about 1 km east of Piojo Airstrip, Hunter-Liggett Military Reservation, *Norris 87249, 87251, & 87252*; Santa Cruz Co.: Englesman Loop Trail, Wilder Ranch State Park, *Kellman 2254* (CAS) and Yellow Bank Creek near Highway 1, *Kellman 2091* (CAS).

***Microbryum starkeanum* (Hedwig) Zander**
[Pottiaceae]

Literature: Kellman 2003; Shevock and Toren 2001. As *Anacalypta starkeana* Lesquereux 1868. As *Pottia arizonica* Harthill et al. 1979; Koch 1950a; McCleary 1972; Steere 1954. As *Pottia arizonica* var. *mucronulata* Crum 1957; Flowers 1973. As *Pottia fosbergii* Bartram 1930; Koch 1950a. As *Pottia starkeana* Brandege 1891; Howe 1896, 1897; Harthill et al. 1979; Koch 1950a; Lesquereux 1868; Lesquereux and James 1884; Toren 1977; Watson 1880; Whittemore and Sommers 1999. As *Pottia texana* Crum 1969; Crum and Anderson 1981.

Illustrations: Flowers 1973; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, DMoj, DSon, SN, SW.

Selected specimens: Alameda Co.: Del Valle Road at the eastern border of Del Valle Regional Park about 10 miles south of Livermore, *Whittemore 3361* (MO) [determined by Zander]; Fresno Co.: Dinkey-Trimmer Road east of Haslett Basin, Sierra National Forest, *Norris, Shevock, & Barahona 87476 & 87477*; Lake Co.: near Hell's Peak, *Toren 786* (SFSU, UC); Riverside Co.: below Bighorn Overlook along Highway 74, eastern boundary of San Bernardino National Forest, *Norris 57836*, and 8 miles west of Desert Center on road to Twenty-Nine Palms, *Norris 57930*; San Diego Co.: Box Willow Canyon Campground, Anza Borrego State Park, *Norris 77718 & 77734*; San Luis Obispo Co.: Lynch Canyon Road about 3 miles from Interlake Road south of San Antonio Reservoir, *Norris 85171*; San Mateo Co.: Edgewood Trail, Edgewood County Park, *Whittemore 5345* (MO); Tehama Co.: Antelope Creek Canyon about 10 miles east of Red Bluff along Bell Mine Road, *Berti 419a* (UC).

***Mielichhoferia elongata* (Hoppe & Hornschuch in W. J. Hooker) Nees & Hornschuch**
[Mielichhoferiaceae]

Literature: Brassard and Hedderson 1989; Hartman 1969; Kellman 2003; Shaw 1994a, 1994b. As

Mielichhoferia mielichhoferiana Andrews 1932a; Crum 1957; Schofield 1959; Shaw et al. 1992. As *Mielichhoferia mielichhoferi* McGrew 1976. As *Mielichhoferia* sp. Thomson and Ketchledge 1958. **Illustrations:** Crum 1957; Shacklette 1967; Smith 1978.

Notes: Based on DNA studies conducted by Jon Shaw, this taxon is worthy of recognition at the species level. All specimens attributed as *Mielichhoferia mielichhoferiana* or *M. mielichhoferi* from California are this taxon.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Fresno Co.: Secate Ridge, Pine Flat Reservoir, Sierra National Forest, *Shevock & York 12604*; Humboldt Co.: Highway 96 near Skunk Creek about 3 miles south of Weitchpec, *Norris 58310*; Lake Co.: sulfur hot spring near Anderson Springs, *Toren & Dearing 7256* (CAS); Marin Co.: Pt. Reyes Bird Observatory about 5 miles north of Bolinas, *Robertson 1690a* (CAS); Mariposa Co.: Highway 140 near El Portal, *Shevock 19511*; Nevada Co.: Shady Creek between Nevada City and North San Juan, *Toren 1807* (SFSU, UC); Placer Co.: Drum Powerhouse Road between Dam and town of Dutch Flat, Tahoe National Forest, *Shevock & Norris 20668*; Santa Cruz Co.: Greyhound Rock, Highway 1, *Shevock & Ng 18442*; Trinity Co.: Highway 299 near junction to Old Helena, Trinity River, Shasta-Trinity National Forest, *Shevock, Lin, & Chen 17740*.

***Mielichhoferia tehamensis* Showers**

[Mielichhoferiaceae]

Literature: Brassard and Hedderson 1983; Showers 1980, 1982.

Illustrations: Showers 1980.

Geographic subdivisions: CaR.

Selected specimens: Shasta Co.: Lassen Volcanic National Park, Crescent Cliffs, *Showers 3904* (CAS), West Fork Hat Creek, *Showers 3644* (SFSU), Pilot Pinnacle, *Showers 3769* (SFSU), Brokeoff Mountain, *Showers 2745* (SFSU); Tehama Co.: Mt. Conard, Lassen Volcanic National Park, *Showers 3350* (CAS, MICH, SFSU).

****Mnium arizonicum* Amann** [Mniaceae]

Illustrations: Flowers 1973; Koponen 1972; Lawton 1971; Sharp et al. 1994. See also Bowers 1969.

Geographic subdivisions: MP, SN, SNE.

Selected specimens: Inyo Co.: near Hearst Lake on trail from Onion Valley to Kearsarge Pass, John Muir Wilderness, Inyo National Forest, *Norris 46758*; Modoc Co.: north end Patterson Lake, South Warner Wilderness, Modoc National Forest, *Harpel 2250* (pers. herb.); Tulare Co.: Cabin Creek Meadow near General's Highway, Sequoia National Park, *Dennis s.n.* (CAS, UC).

****Mnium blyttii* Bruch & W. P. Schimper**

[Mniaceae]

Illustrations: Flowers 1973; Lawton 1971.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Alpine Co.: near Winnemucca Lake, Mokelumne Wilderness, Eldorado National Forest, *Norris 71207*; Shasta Co.: lava tube near Old Station, Hat Creek Valley, Lassen Volcanic National Park, *Showers 1931* (UC); Siskiyou Co.: Canyon Creek, Marble Mountain Wilderness, Klamath National Forest, *Tucker 3776* (UC) [determined by Steere]; Tulare Co.: headwaters of the Little Kern River, Golden Trout Wilderness, Sequoia National Forest, *Norris 67937 & 67945*.

***Mnium marginatum* (Dickson ex Withering)**

Palisot de Beauvois [Mniaceae]

Literature: Crum and Anderson 1981; Flowers 1973; Harthill et al. 1979; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Showers 1982.

Illustrations: Abramov and Volkova 1998; Allen 2002; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CW, NW, SN, SNE, SW.

Selected specimens: Alpine Co.: Silver Creek at Carson River, Toiyabe National Forest, *Norris 78983* and near Winnemucca Lake, Mokelumne Wilderness, Eldorado National Forest, *Norris 71258*; El Dorado Co.: Highway 50 along South Fork American River at Bridal Veil Falls Campground, Eldorado National Forest, *Norris 58402*; Fresno Co.: Cedar Grove at Sheep Creek, South Fork Kings River, Kings Canyon National Park, *Shevock 13753*; Mono Co.: Lee Vining Creek about 0.5 mile above Highway 395, *Koch 1766* (MO, UC); Riverside Co.: Indian Creek above UC James Reserve, San Jacinto Mountains, San Bernardino National Forest, *Harpel 1397* (pers. herb.); Santa Cruz Co.: Big Creek near Davenport, *Kellman 1500* (CAS); Siskiyou Co.: Long Gulch Lake southwest of Callahan, Klamath National Forest, *Norris 57527*.

***Mnium spinulosum* Bruch & W. P. Schimper**

[Mniaceae]

Literature: Lesquereux 1868.

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Koponen 1973b; Lawton 1971.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Del Norte Co.: slopes above Whiskey Lake, Siskiyou National Forest, *Norris 57725*; Fresno Co.: Taboose Pass Trail, headwaters of South Fork Kings River, Kings Canyon National Park, *Shevock 13851*; Inyo Co.: slopes above Treasure Lake west of Big Pine, John Muir Wilderness, Inyo National Forest, *Norris 46951*; Siskiyou Co.: about 1 mile east of Copper Butte, *Norris 50218*; Tehama Co.: fork of Beegum Creek off of Forest Road 35 about 1.5 miles west of Rat Trap Gap, Shasta-Trinity National Forest, *Norris 57003*.

***Mnium thomsonii* W. P. Schimper** [Mniaceae]

Literature: Crum and Anderson 1981; McGrew 1976. As *Mnium orthorrhynchum* Koch 1950a; Showers 1982; Spjut 1971.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Koponen 1972; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN, SNE.

Selected specimens: El Dorado Co.: Silver Fork Campground along Silver Fork American River, Eldorado National Forest, *Norris* 82915; Fresno Co.: Grizzly Creek at junction with South Fork Kings River along Highway 180, Sequoia National Forest, *Shevock* 12445; Lake Co.: Alder Creek, Cobb Mountain, *Toren & Dearing* 7089 (CAS) [determined by Wyatt]; Marin Co.: trail near Mud Lake, Point Reyes National Seashore, *Norris* 71833; Mono Co.: Lundy Lakes Trail along Mill Creek, Toiyabe National Forest, *Norris* 78903; Tuolumne Co.: Mill Creek below Cascade Creek Campground, Stanislaus National Forest, *Norris* 78823.

***Molendoa sendtneriana* (Bruch & W. P. Schimper) Limpricht** [Pottiaceae]

Literature: Zander 1977a. As *Anoetangium obtusifolium* Harthill et al. 1979; McCleary 1972; Steere 1954.

Illustrations: Allen 2002; Ignatov and Ignatova 2003; Iwatsuki and Sharp 1958; Saito 1975; Sharp et al. 1994.

Geographic subdivisions: SN, SW.

Selected specimens: Los Angeles Co.: near White's Landing, Santa Catalina Island, *Steere* s.n. (UBC); Placer Co.: Bowman Lake west of Truckee, *Norris* 76949.

****Myurella julacea* (Schwägrichen in Schultes) Bruch & W. P. Schimper** [Pterigynandraceae]

Illustrations: Ignatov et al. 1996; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: SNE.

Selected specimens: Inyo Co.: slopes near Dragon Peak near Onion Valley, John Muir Wilderness, Inyo National Forest, *Norris* 46751b and Lake Sabrina Basin, Inyo National Forest, *Shevock* 15288.

***Neckera douglasii* W. J. Hooker** [Neckeraceae]

Literature: Bourell 1981; Bradshaw 1926; Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Smith 1970; Thomson and Ketchledge 1958; Watson 1880; Yurky 1990, 1995.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, CW, NW.

Selected specimens: Lake Co.: Bucknell Creek north of Horse Mountain, Mendocino National Forest, *Toren* 7453a (CAS); Marin Co.: trail near Mud Lake, Point Reyes National Seashore, *Norris* 71817; Mendocino Co.: County Road 409 about 1 mile east of Highway 1 south of Fort Bragg, *Norris*

11711; Santa Barbara Co.: Hollister Ranch, Gaviota Coast, *P. Huebner* s.n. (SBBG); Santa Cruz Co.: Opal Creek, Big Basin Redwood State Park, *Kellman* 1008 (CAS); Shasta Co.: Dog Creek Road about 3 miles west of Interstate 5, *Norris & Hermann* 22538; Siskiyou Co.: Elk Creek at Malone Creek south of Happy Camp, *Norris* 52232.

***Oncophorus virens* (Hedwig) Bridel** [Dicranaceae]

Literature: Cooke 1941; Crum and Anderson 1981; Flowers 1973; Holmberg 1969; Koch 1950a, 1958; Lawton 1971; McGrew 1976; Showers 1982; Spjut 1971. As *Dicranum virens* var. *compactum* Lesquereux and James 1884. As *Dicranum virens* var. *serratum* Lesquereux 1868; Watson 1880.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: El Dorado Co.: Round Meadow about 3 miles southeast of Sayles Canyon Trailhead, Eldorado National Forest, *Norris* 71056 & 71060; Fresno Co.: outlet of fifth Baxter Lake, Kings Canyon National Park, *Shevock & York* 16582; Humboldt Co.: Kneeland, *Tracy* 14806 (UC); Mono Co.: Mildred Lake about 3 miles above Convict Lake, John Muir Wilderness, Inyo National Forest, *Norris* 71396 and Gardisky Lake west of Lee Vining, Inyo National Forest, *Norris* 104209; Siskiyou Co.: Waterdog Lake, Klamath National Forest, *McGrew* 493 (UC).

****Oncophorus wahlenbergii* Bridel** [Dicranaceae]

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: SN, SNE.

Selected specimens: Inyo Co.: Baxter Pass Trail, Bighorn Sheep Zoological Area, John Muir Wilderness, Inyo National Forest, *Shevock & York* 16613 and trail from Onion Valley to Robinson Lake west of Independence, Inyo National Forest, *Norris* 46670 and slopes above George Lake west of Bishop, John Muir Wilderness, Inyo National Forest, *Norris* 71437.

***Orthodicranum tauricum* (Sapelin) Smirnova** [Dicranaceae]

Literature: Shevock and Toren 2001. As *Dicranum strictum* Howe 1896; Lesquereux 1868; Thomson and Ketchledge 1958; Watson 1880. As *Dicranum tauricum* Bourell 1981; Flowers 1973; Holmberg 1969; Jamieson 1969; Kellman 2003; Lawton 1971; McGrew 1976; Showers 1982; Smith 1970; Spjut 1971; Toren 1977; Yurky 1990. As *Orthodicranum strictum* Koch 1950a, 1951e; Koch and Ikenberry 1954.

Illustrations: Abramov and Volkova 1998; Enroth 1989; As *Dicranum tauricum* Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Del Norte Co.: between Wilderness Falls to Doe Flat, *Norris* 67761; El Dorado Co.: Sly Park Creek, *Norris* 58574; Marin Co.: Cataract Trail near Alpine Lake, *Yurky* 1050 (SFSU); Mendocino Co.: Highway 101 at Cummings turn-off, milepost 84.91, *Norris* 21639; Santa Cruz Co.: Zayante Canyon Road north of Felton, *Norris* 86874; Siskiyou Co.: Cedar Basin, South Fork Sacramento River, Shasta-Trinity National Forest, *Shevock* 12227; Tulare Co.: Redwood Mountain Grove, trail at Redwood Creek, Kings Canyon National Park, *Shevock* 17483.

***Orthodontium gracile* (Wilson in J. E. Smith) Schwägrichen ex Bruch & W. P. Schimper**
[Orthodontiaceae]

Literature: Christy and Wagner 1996; Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a, 1951d; Lawton 1971; Smith 1970; Steere et al. 1954; Yurky 1990, 1995. As *Stableria gracilis* Andrews 1932b; Howe 1897. As *Stableria gracilis* var. *californica* Andrews 1932b; Howe 1897.

Illustrations: Andrews 1935; Lawton 1971; Meijer 1951; Sharp et al. 1994. As *Stableria gracilis* Brotherus 1924–1925.

Geographic subdivisions: CW, NW.

Selected specimens: Del Norte Co.: Damnation Creek Trail, Del Norte Coast Redwoods State Park, *Norris* 46231; Humboldt Co.: Foothill Trail, Prairie Creek Redwoods State Park, *Norris* 46024; Marin Co.: Sir Francis Drake Blvd. Near Nicasio Valley Road, *Robertson s.n.* (CAS); Monterey Co.: Big Sur River, Big Sur State Park, *Koch* 3662 (MO, UC); Mendocino Co.: about 2 miles east of Fort Bragg, *Norris* 12041; San Mateo Co.: near Little Butano Creek, Butano State Park, *Whittemore* 4016 (MO); Santa Cruz Co.: Forest of Nisene Marks State Park south of Santa Cruz, *Norris* 55640 & 55644; Sonoma Co.: Forest Theatre, Armstrong Grove, Redwood Park, *Koch* 3466 (UC).

***Orthodontium pellucens* (W. J. Hooker) Bruch & W. P. Schimper in C. Müller Hal.**
[Orthodontiaceae]

Literature: Crum and Anderson 1981; Holmberg 1969; Koch 1949a, 1950a.

Illustrations: Crum and Anderson 1981; Sharp et al. 1994.

Geographic subdivisions: CW, NW.

Selected specimens: Del Norte Co.: Stout Memorial Grove, Jedediah Smith Redwoods State Park, *Koch* 3809 (UC); Humboldt Co.: near Elk Grove Park Headquarters, Prairie Creek Redwoods State Park, *Shevock* 16735 and along Prairie Creek, *Norris* 68375; Monterey Co.: Big Sur State Park, *Bartlett* 3 (UC).

***Orthotrichum affine* Schader ex Bridel**
[Orthotrichaceae]

Literature: Flowers 1973; Harpel 1980a; Harthill et al. 1979; Koch 1950a; Lawton 1971; Moxley

1937; Showers 1982; Spjut 1971; Steere et al. 1954; Yurky 1990, 1995.

Illustrations: Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971; Smith 1978; Vitt 1973.

Geographic subdivisions: CaR, MP, NW, SN, SW.

Selected specimens: Mendocino Co.: road to Plaskett Meadows about 1 mile south of Mendocino Pass, Mendocino National Forest, *Norris* 19570; Modoc Co.: road to Whitehorse Flat about 3 miles north of Day, Shasta-Trinity National Forest, *Norris* 84733; Sierra Co.: Highway 49 between Bassetts and Sierra City, Tahoe National Forest, *Kellman* 262 (CAS); Trinity Co.: Rush Creek about 1 mile below Rush Creek Lakes, Trinity Alps Wilderness, Shasta-Trinity National Forest, *Norris* 85377; Tulare Co.: Forest Trail 31E18 at Galena Creek, Sequoia National Forest, *Shevock* 9080; Ventura Co.: Potrero John Creek near Highway 33, Los Padres National Forest, *Norris* 55525.

***Orthotrichum alpestre* Hornschuch ex Bruch & W. P. Schimper** [Orthotrichaceae]

Literature: Flowers 1973; Harpel 1980a; Harthill et al. 1979; Koch 1950a; McGrew 1976; Showers 1982; Spjut 1971; Strid 1974; Watson 1880.

Illustrations: Flowers 1973; Ignatov and Ignatova 2003; Ignatov and Lewinsky-Haapasaari 1994; Lawton 1971; Vitt 1973.

Geographic subdivisions: CaR, MP, NW, SN, SNE, SW.

Selected specimens: Alpine Co.: Silver Creek at Carson River, Toiyabe National Forest, *Norris* 78959; Lassen Co.: Termo-Grasshopper Road about 12 miles west of Termo, *Norris & Hermann* 22641; San Diego Co.: about 1 mile north of Cuyamaca State Park Headquarters, *Norris* 50729; Siskiyou Co.: about 1 mile south of Big Flat, *Norris* 9228; Tulare Co.: just north of Kennedy Meadows Campground adjacent to the South Fork Kern River, South Sierra Wilderness, Inyo National Forest, *Shevock* 14805; Tuolumne Co.: Herring Creek Road below Forest Service Road 4N12, west-northwest of Strawberry, Stanislaus National Forest, *Norris* 100420.

***Orthotrichum bolanderi* Sullivan**
[Orthotrichaceae]

Literature: Harthill et al. 1979; Kingman 1912; Koch 1950a; Koch and Ikenberry 1954; Lesquerieux and James 1884; Long 1978; Steere et al. 1954; Thomson and Ketchledge 1958; Toren 1977; Watson 1880; Yurky 1990, 1995.

Illustrations: Sharp et al. 1994; Vitt 1973.

Geographic subdivisions: CaR, CW, NW, SN, SW.

Selected specimens: Butte Co.: Big Chico Creek at northeast boundary of Bidwell Park, *Norris* 70085; Monterey Co.: Salmon River bridge south of Pinnacles, Hunter-Liggett Military Reservation, *Norris* 87316; Placer Co.: Clover Valley Creek at Sierra College Road, *Norris* 81945; Riverside Co.: Mesa de Colorado, Santa Rosa Plateau, southern Santa Ana Mountains, *Shevock* 4273; Sonoma Co.:

summit ridge behind Armstrong Park, *Koch 3534* (UC); Tulare Co.: Elk Creek near Potwisha Campground, Middle Fork Kaweah River, Sequoia National Park, *Shevock, Norris, & Barahona 13184*.

***Orthotrichum consimile* Mitten** [Orthotrichaceae]

Literature: Harthill et al. 1979; Holmberg 1969; Howe 1896; Jamieson 1969; Koch 1950a; Lawton 1971; Lesquereux 1868; Moxley 1928; Shevock and Toren 2001; Yurky 1990, 1995. As *Orthotrichum columbicum* Lesquereux 1868.

Illustrations: Lawton 1971; Lewinsky-Haapasaari et al. 1995; Vitt 1973.

Geographic subdivisions: CW, NW.

Selected specimens: Del Norte Co.: French Hill Road about 2.5 miles above Highway 199 southwest of Gasquet, Six Rivers National Forest, *Norris 85053*; Humboldt Co.: Blue Lake, *Howe 1016* (UC) and Arcata Community Forest, *Silver 731* (UC); Lake Co.: Summit Lake near Mt. Sanhedrin, Mendocino National Forest, *Toren & Dearing 7212* (CAS); Marin Co.: Olema, Point Reyes National Seashore, *Howe 74 & 81* (UC); San Francisco Co.: Panhandle of Golden Gate Park, *Shevock 18932*.

***Orthotrichum cupulatum* G. F. Hoffman ex Bridel** [Orthotrichaceae]

Literature: Bourell 1981; Flowers 1973; Kellman 2003; Koch 1950a; Lesquereux 1868; Toren 1977; Watson 1880.

Illustrations: Flowers 1973; Ignatov and Ignatova 2003; Ignatov and Lewinsky-Haapasaari 1994; Lawton 1971; Sharp et al. 1994; Smith 1978; Vitt 1973.

Geographic subdivisions: CaR, CW, MP, NW, SN, SNE.

Selected specimens: Alpine Co.: Silver Creek at Carson River, Toiyabe National Forest, *Norris 78988*; Fresno Co.: Boyden Cave adjacent to South Fork Kings River and Highway 180, Sequoia National Forest, *Shevock & York 17200*; Lake Co.: Summit Springs Trail, Snow Mountain Wilderness, Mendocino National Forest, *Toren & Dearing 7521* (CAS); Humboldt Co.: near Showers Pass, *Norris 8654*; Mendocino Co.: Ukiah Hot Springs, *Bolander s.n.* (UC); Santa Cruz Co.: Blue Cliff, Fall Creek, Division of Henry Cowell State Park, *Kellman 657* (CAS); Shasta Co.: Fall Creek Road about 1 mile southeast of McCloud Bridge at Shasta Lake, Shasta-Trinity National Forest, *Norris 84870* and Highway 299 about 1 mile south of Montgomery Creek, *Norris 68598*.

***Orthotrichum diaphanum* Schrader ex Bridel** [Orthotrichaceae]

Literature: Kellman 2003; Shevock and Toren 2001.

Illustrations: Ignatov and Ignatova 2003; Lewinsky 1984; Sharp et al. 1994; Smith 1978; Vitt 1973.

Geographic subdivisions: CW, SW.

Selected specimens: Alameda Co.: UC Berkeley Campus, *Norris 100334*; Los Angeles Co.: Me-

morial Park, Claremont, *Harpel 890* (pers. herb.); San Bernardino Co.: Paris Hill City Park, City of San Bernardino, *Harpel 1688* (pers. herb.); San Diego Co.: El Monte Road about 1 mile east of El Monte Park, *Norris & Piippo 82150* and San Clemente Canyon at Genesee Road, City of San Diego, *Norris 50712*; San Francisco Co.: Panhandle, Golden Gate Park, *Toren 7795* (CAS) and *Shevock 18931*; Santa Cruz Co.: San Lorenzo Park, City of Santa Cruz, *Kellman 967* (CAS).

***Orthotrichum euryphyllum* Venturi in Röhl** [Orthotrichaceae]

Literature: Lewinsky-Haapasaari and Norris 1998a. As *Orthotrichum epapillosum* Lawton and Hermann 1973.

Illustrations: Lewinsky-Haapasaari and Norris 1998a.

Geographic subdivisions: CaR, MP.

Selected specimens: Lassen Co.: small creek west of Highway 395 about 1 mile south of Lassen-Modoc county line, *Norris 84742*; Modoc Co.: Forest Road 46 at Boles Creek southeast of Clear Lake, Modoc National Forest, *Norris 79167a*; Shasta Co.: Cassel-Fall River Road about 2 miles south of Fall River Mills, *Norris 84701*; Tehama Co.: Highway 36 northeast of Red Bluff about 2 miles west of Dales, *Norris 56021*.

***Orthotrichum flowersii* Vitt** [Orthotrichaceae]

Literature: Galloway 1978; Harpel 1980a; Harthill et al. 1979.

Illustrations: Vitt 1971, 1973.

Geographic subdivisions: DMoj, SN, SNE, SW.

Selected specimens: Kern Co.: Black Gulch near Lake Isabella, Sequoia National Forest, *Norris & Piippo 82204*; Los Angeles Co.: Black Jack Campground at base of Orizaba Mountain, Santa Catalina Island, *Shevock & Thorne 4073*; Riverside Co.: USFS Guard Station, San Jacinto Mountains, San Bernardino National Forest, *Harpel 994* (pers. herb.); San Bernardino Co.: Paris Hill City Park, City of San Bernardino, *Harpel 658* (pers. herb.); San Diego Co.: Highway 94 at junction to Outdoor World Campground about 3 miles east of La Pasta Road, *Norris 77797*; Tulare Co.: South Creek just above South Creek Falls off of County Road M-99 north of Kernville, Sequoia National Forest, *Norris 87078* and South Fork Kaweah River near Clough Cave, Sequoia National Park, *Norris & Shevock 92730*.

***Orthotrichum hallii* Sullivant & Lesquereux in Sullivant** [Orthotrichaceae]

Literature: Stark and Whittemore 1992.

Illustrations: Flowers 1973; Lawton 1971; Sharp et al. 1994; Vitt 1973.

Geographic subdivisions: CaR, DMoj, NW, SN, SNE, SW.

Selected specimens: Kern Co.: Scodie Mountains northeast of Pinyon Peak about 1 mile west of Walker Pass off of Highway 178, *Norris 87127*;

Lake Co.: near Round Mountain, Knoxville BLM Recreation Area, *Toren & Dearing* 7058 (CAS); San Bernardino Co.: Curtis Canyon, Clark Mountain Wilderness, Mojave National Preserve, Mojave Desert, *Shevock, Spence, Glazer, & Laeger* 23668; Shasta Co.: Cassel-Fall River Road about 2 miles south of Fall River Mills, *Norris* 84724; Trinity Co.: Bridge Gulch at Natural Bridge, Shasta-Trinity National Forest, *Norris* 67734; Tulare Co.: trail to Crystal Cave near Cascade Creek, Sequoia National Park, *Shevock & Tseng* 15768; Ventura Co.: Howard Creek Trail about 1 mile east of Highway 33, Los Padres National Forest, *Norris* 55512.

****Orthotrichum holzingeri* Renauld & Cardot in Holzinger** [Orthotrichaceae]

Illustrations: Lawton 1971; Vitt 1973, 1991.

Geographic subdivisions: MP, SN.

Selected specimens: Modoc Co.: Modoc National Forest, Highway 139 at Biles Road about 13 miles northwest of Canby, *Norris* 70467 and Forest Road 46 at Boles Creek southeast of Clear Lake, Modoc National Forest, *Norris* 79166 & 79167b; Tuolumne Co.: Middle Fork Tuolumne River at Middle Fork Campground, *Norris & Shevock* 103989.

***Orthotrichum laevigatum* J. E. Zetterstedt** [Orthotrichaceae]

Literature: Flowers 1973; Harpel 1980a; Harthill et al. 1979; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Long 1978; McGrew 1976; Mishler 1978; Showers 1982; Sigal 1975; Spjut 1971; Toren 1977. As *Orthotrichum kingianum* Lesquereux 1868; Lesquereux and James 1884; Watson 1880. As *Orthotrichum roellii* Koch 1950a.

Illustrations: Flowers 1973; Ignatov and Lewinsky-Haapasaari 1994; Lawton 1971; Vitt 1973.

Geographic subdivisions: CaR, MP, NW, SN, SNE, SW.

Selected specimens: Colusa Co.: Summit Springs south of Snow Mountain, Mendocino National Forest, *Norris* 76126; Inyo Co.: about 3 miles south of Schulman Grove, White Mountains, Inyo National Forest, *Norris* 46857; Lake Co.: Cobb Mountain Summit, *Toren & Dearing* 7387 (CAS); Lassen Co.: Amedee Canyon north of Honey Lake, *Norris* 81028; San Bernardino Co.: west end Bluff Lake, San Geronio Wilderness, San Bernardino National Forest, *Harpel* 599 (pers. herb.); Shasta Co.: Pit River about 2 miles below powerhouse #2, Shasta-Trinity National Forest, *Norris* 82591; Tulare Co.: Trail 34E08 southeast of Manter Meadow near Black Mountain, Domeland Wilderness, Sequoia National Forest, *Shevock* 10827.

***Orthotrichum lyellii* W. J. Hooker & Taylor** [Orthotrichaceae]

Literature: Bourell 1981; Bradshaw 1926; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Kingman 1912; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquer-

aux 1868; McCleary 1972; Millspaugh and Nuttall 1923; Mishler 1978; Sayre 1940; Shevock and Toren 2001; Showers 1982; Sigal 1975; Smith 1970; Spjut 1971; Steere 1954; Steere et al. 1954; Sullivant 1856; Thomson and Ketchledge 1958; Toren 1977; Watson 1880; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Orthotrichum lyellii* var. *howei* Cardot and Thériot 1900.

Illustrations: Lawton 1971; Sharp et al. 1994; Smith 1978; Vitt 1973.

Geographic subdivisions: CaR, CW, DMoj, NW, SN, SW.

Selected specimens: Contra Costa Co.: Mt. Diablo, *Brewer* 844 (UC); Kern Co.: Cedar Creek along Highway 155, west of Greenhorn Summit, Greenhorn Mountains, Sequoia National Forest, *Shevock* 10790; Lake Co.: Highway 53 about 1 mile south of Highway 20, *Norris* 47692; San Diego Co.: Heise County Park south of Julian, *Norris* 50739; Santa Cruz Co.: Laurel Road at Highway 17, *Kellman* 2712 (CAS); Siskiyou Co.: Duck Lake Trail near Parrott's Mill Road, Klamath National Forest, *Norris* 22805.

***Orthotrichum macounii* Austin** [Orthotrichaceae]

Literature: Spjut 1971.

Illustrations: Flowers 1973.

Geographic subdivisions: NW.

Selected specimens: Siskiyou Co.: above Big Boulder Lake west of Carrville, Klamath National Forest, *Norris & Streimann* 74797.

***Orthotrichum obtusifolium* Bridel**

[Orthotrichaceae]

Literature: Kellman 2003; Toren 1977. As *Stroemia obtusifolia* Koch 1951b.

Illustrations: Ignatov and Ignatova 2003; Ignatov and Lewinsky-Haapasaari 1994; Ireland 1982; Lawton 1971; Smith 1978; Vitt 1973.

Geographic subdivisions: CaR, CW, MP, NW, SN.

Selected specimens: Fresno Co.: Redwood Creek at Windy Gulch Grove, Sequoia National Forest, *Norris, Shevock, & Barahona* 87949; Lake Co.: Crockett Peak, Snow Mountain Wilderness, Mendocino National Forest, *Toren & Dearing* 5346a (CAS); Modoc Co.: Cottonwood Flat Campground, Modoc National Forest, *Norris* 68517 & 68522; Santa Cruz Co.: Gray Whale Ranch, Wilder Ranch State Park, *Kellman* 963 (CAS); Shasta Co.: Casberry Flat about 1 mile west of Hatchett Mountain Summit, *Norris* 68588; Siskiyou Co.: Salmon River about 1 mile south of Big Flat, *Norris* 9201 (determined by Vitt); Tehama Co.: Seven Mile Creek along Highway 36 at milepost 48 east of Red Bluff, *Norris* 21265; Tulare Co.: Deep Creek, Little Kern River, Golden Trout Wilderness, Sequoia National Forest, *Norris* 67914.

****Orthotrichum pallens* Bruch ex Bridel**

[Orthotrichaceae]

Illustrations: Flowers 1973; Ignatov and Ignatova 2003; Ignatov and Lewinsky-Haapasaari 1994; Lawton 1971; Sharp et al. 1994; Vitt 1973.

Geographic subdivisions: SNE.

Selected specimens: Mono Co.: above Robinson Lake on trail to Barney Creek and Twin Lakes, Toiyabe National Forest, *Norris* 99646.

***Orthotrichum papillosum* Hampe**

[Orthotrichaceae]

Literature: Kellman 2003; Koch 1950a. As *Orthotrichum lyellii* var. *papillosum* Jamieson 1969; Koch 1958; Lesquereux and James 1884.

Illustrations: As *O. lyellii* Lawton 1971.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: El Dorado Co.: Highway 193 at Garden Valley Road, *Norris* & *Piippo* 82304; Humboldt Co.: Forest Road 10N01 at Mill Creek, Six Rivers National Forest, *Norris* 70573; Lake Co.: Forest Road M-3 at Low Gap, Mendocino National Forest, *Shevock*, *Bourell*, & *Toren* 15858; Mendocino Co.: Pygmy Forest near Albion, *Shevock* & *Allen* 21921; Monterey Co.: Pfeiffer-Big Sur State Park at campground, *Norris* 75903; Santa Cruz Co.: Quail Hollow Ranch County Park, *Kellman* 131 (UC); Shasta Co.: Indian Springs, Castle Crags State Park, *Norris* 103043; Siskiyou Co.: McCloud River about 5 miles east of McCloud, *Norris* & *Hillyard* 103896; Sonoma Co.: Bodega Marine Laboratory, *Norris* 103461; Tulare Co.: South Fork Tule River near Camp Nelson, *Norris*, *Shevock*, & *Barahona* 87669.

***Orthotrichum pellucidum* Lindberg**

[Orthotrichaceae]

Literature: Howe 1896.

Illustrations: Ignatov and Lewinsky-Haapasaari 1994; Vitt 1973. As *Orthotrichum cupulatum* var. *jamesianum* Lawton 1971. As *Orthotrichum jamesianum* Flowers 1973; McGrew 1976.

Geographic subdivisions: CaR, MP, NW, SN.

Selected specimens: Kern Co.: Erskine Creek Canyon about halfway between canyon entrance and Liebel Ranch, Piute Mountains, *Shevock* 13363; Modoc Co.: Crowder Flat about 2 miles south of Oregon border, *Norris* 79151; Tehama Co.: Anthony Peak, Mendocino National Forest, *Norris* 55026 and Tomhead Gulch, Shasta-Trinity National Forest, *Norris* 56912; Tulare Co.: Coy Flat Road near bridge crossing of Middle Fork Tule River, Camp Nelson, Sequoia National Forest, *Norris*, *Shevock*, & *Barahona* 87688.

****Orthotrichum praemorsum* Venturi**

[Orthotrichaceae]

Illustrations: Lawton 1971; Vitt 1973.

Geographic subdivisions: SNE.

Selected specimens: Mono Co.: Highway 89 near junction with Highway 395, *Shevock* & *Glazer* 21800.

***Orthotrichum pulchellum* Brunton in J. E.**

Smith [Orthotrichaceae]

Literature: Lesquereux 1868; Watson 1880.

Illustrations: Lawton 1971; Smith 1978; Vitt 1973.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: near mouth of Damnation Creek, Del Norte Redwoods State Park, *Norris* 10974 & 48230; Humboldt Co.: near Abalone Point, Patricks Point State Park, *Norris* 23920 and College Cove about 0.5 mile north of Trinidad, *Norris* 47742.

***Orthotrichum pumilum* Swartz** [Orthotrichaceae]

Literature: Harpel 1980a, 1980b.

Illustrations: Ignatov and Ignatova 2003; Ignatov and Lewinsky-Haapasaari 1994; Lawton 1971; Vitt 1973.

Geographic subdivisions: CaR, NW, SN, SW.

Selected specimens: Lake Co.: Highway 53 about 1 mile south of Highway 20, *Norris* 47673 and Upper Lake Ranger Station, Mendocino National Forest, *Toren* 7436a (CAS) [determined by Vitt]; Orange Co.: Harding Canyon about 0.5 mile north of Mojeska Canyon and Tucker Bird Sanctuary, Cleveland National Forest, *Shevock* 4003; San Bernardino Co.: Waterman Canyon, San Bernardino National Forest, *Harpel* 2398 (pers. herb.); Santa Barbara Co.: about 1 mile south of Bates Canyon Campground, *Norris* 55381; Shasta Co.: County Road A16 about 14 miles east of Platina, *Norris* 23764; Tulare Co.: Highway 190 at Moorehouse Springs Creek, Sequoia National Forest, *Norris* 50924 and between Posey to White River, *Kellman* 1453 (CAS).

***Orthotrichum pylaisii* Bridel** [Orthotrichaceae]

Literature: Harthill et al. 1979; McGrew 1976; Showers 1982. As *Orthotrichum microblepharum* Spjut 1971.

Illustrations: Vitt 1973.

Geographic subdivisions: CaR, MP, NW, SN.

Selected specimens: Alpine Co.: Red Lake Creek, Toiyabe National Forest, *Norris* 88197; Fresno Co.: Spanish Mountain Jeep Road, Sierra National Forest, *Shevock* & *York* 12429; Humboldt Co.: Grouse Mountain Road about 3 miles northeast of Horse Mountain Road, Six Rivers National Forest, *Norris* 45777; Modoc Co.: Big Sage Reservoir north of Alturas, *Norris* 68497; Siskiyou Co.: McCloud River about 5 miles east of McCloud, *Norris* & *Hillyard* 103897; Trinity Co.: below Packer's Peak, *Norris* 8982.

***Orthotrichum rivulare* Turner** [Orthotrichaceae]

Literature: Bourell 1981; Holmberg 1969; Howe 1896; Kellman 2003; Koch 1950a, 1951e; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Shevock and Toren 2001; Spjut 1971; Steere et al. 1954; Thomson and Ketchledge 1958; Watson 1880.

Illustrations: Lawton 1971; Lewinsky-Haapasaari and Norris 1998a; Smith 1978; Vitt 1973.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Del Norte Co.: Smith River at Highway 199 about 9 miles east of junction with Highway 101, Six Rivers National Forest, *Norris*

85007; Fresno Co.: Big Creek at Blue Canyon, Sierra National Forest, *Norris, Shevock, & Barahona* 87438; Mendocino Co.: Greenwood Ridge Road at Navarro River near entrance to Hendy Redwoods State Park, *Norris* 53107; Santa Cruz Co.: San Lorenzo River, Henry Cowell Redwoods State Park, *Kellman* 447 (CAS); Shasta Co.: Highway 299 about 1 mile north of Mineral School at intersection of road to Oak Run, *Norris* 68636; Trinity Co.: Ditch Gulch below Highway 3 about 1 mile north of Highway 36, Shasta-Trinity National Forest, *Norris* 68686; Tulare Co.: off of General's Highway opposite canyon from Inspiration Point, Sequoia National Park, *Shevock, Whitmarsh, & Johnson* 17154.

***Orthotrichum rupestre* Schleicher ex Schwägrichen** [Orthotrichaceae]

Literature: Bourell 1981; Cooke 1941; Harpel 1980a; Harthill et al. 1979; Kellman 2003; Kingman 1912; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Long 1978; McGrew 1976; Mishler 1978; Moxley 1928; Showers 1982; Sigal 1975; Spjut 1971; Steere et al. 1954; Strid 1974; Toren 1977; Watson 1880; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Orthotrichum sturmii* Lesquereux 1868; Lesquereux and James 1884; Watson 1880.

Illustrations: Flowers 1973; Ignatov and Ignatova 2003; Ignatov and Lewinsky-Haapasaari 1994; Lawton 1971; Lewinsky 1987, 1993; Sharp et al. 1994; Smith 1978; Vitt 1973.

Geographic subdivisions: CaR, CW, MP, NW, SN, SNE, SW.

Selected specimens: Fresno Co.: Mist Falls trail near junction with Bubbs Creeek, Kings Canyon National Park, *Shevock & York* 14478; Humboldt Co.: Forest Road 7K100 at junction of road to Horse Mountain Ski Lift, Six Rivers National Forest, *Norris* 70665; Lake Co.: The Openings above Cedar Creek, Mendocino National Forest, *Toren & Shevock* 8093 (CAS); Modoc Co.: west side Goose Lake about 4 miles south of Oregon border, *Norris* 23656; Orange Co.: Upper Trabuco Canyon, Santa Ana Mountains, Cleveland National Forest, *Shevock* 3991; Santa Clara Co.: Mt. Hamilton about 1 mile below summit, *Koch* 1421 (UC).

***Orthotrichum shevockii* Lewinsky-Haapasaari & Norris** [Orthotrichaceae]

Literature: Lewinsky-Haapasaari and Norris 1998b.

Illustrations: Lewinsky-Haapasaari and Norris 1998b.

Geographic subdivisions: SN, SNE.

Selected specimens: Kern Co.: Highway 178 near Chimney Peak Road, base of Scodie Mountains, *Shevock & Tan* 13048 and *Shevock* 17093; Highway 178 west of Canebreak Creek, Scodie Mountains, *Norris* 87128, Pacific Crest Trail, Kiavah Wilderness, Scodie Mountains, Sequoia National

Forest, *Shevock & York* 13398, 13404; Mono Co.: Highway 89 about 3 miles west of junction with Highway 395, Toiyabe National Forest, *Norris* 76506 and along Slinkard Creek off of Highway 89 near junction with Highway 395, *Shevock & Glazer* 21802 and Highway 120, Benton Hills about 2 miles west of Benton, *Shevock & Glazer* 22289.

***Orthotrichum speciosum* Nees in J. W. Sturm** [Orthotrichaceae]

Literature: Harthill et al. 1979; Koch 1950a; Lawton 1971; Lesquereux 1868; McCleary 1972; McGrew 1976; Sayre 1940; Watson 1880; Yurky 1990.

Illustrations: Ignatov and Ignatova 2003; Ignatov and Lewinsky-Haapasaari 1994; Ireland 1982; Lawton 1971; Vitt 1973; Vitt and Darigo 1997.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Del Norte Co.: Doctor Rock, Six Rivers National Forest, *Norris* 57683; El Dorado Co.: South Fork American River at Carpenter Creek, Eldorado National Forest, *Norris* 58427; Marin Co.: Inverness Ridge Trail near Limatour Road, Point Reyes National Seashore, *Yurky* 337 (SFSU); Nevada Co.: Red Mountain on trail from Indian Springs, Tahoe National Forest, *Norris* 102615; Shasta Co.: Soda Creek Road about 3 miles northeast of Interstate 5 near Dunsmuir, Shasta-Trinity National Forest, *Norris* 84773; Siskiyou Co.: Six Mile Creek between Callahan and Cecilville, Klamath National Forest, *Norris* 22964; Tulare Co.: East Fork Kaweah River below Atwell Mills Campground, Sequoia National Park, *Norris* 46493.

***Orthotrichum spjutii* Norris & Vitt** [Orthotrichaceae]

Literature: Norris and Vitt 1993.

Illustrations: Norris and Vitt 1993.

Geographic subdivisions: SN, SNE.

Selected specimens: Mono Co.: near outlet of Kenig Lake, east of Sonora Pass, Toiyabe National Forest, *Norris* 57207 & 57210; Tulare Co.: between BLM Long Valley Campground and South Fork Kern River, Domeland Wilderness, Sequoia National Forest, *Shevock* 15154, 15158, & 15161.

****Orthotrichum striatum* Hedwig** [Orthotrichaceae]

Illustrations: Ignatov and Lewinsky-Haapasaari 1994; Lawton 1971; Smith 1978; Vitt 1973.

Geographic subdivisions: NW, SN.

Selected specimens: Humboldt Co.: Grouse Mountain Road about 3.5 miles northeast of Horse Mountain Road, Six Rivers National Forest, *Norris* 24274 and about 1 mile south of Kneeland Airport, *Norris* 68261; Tulare Co.: East Fork Kaweah River below Atwell Mills Campground, Sequoia National Park, *Norris* 46479 and Buena Vista Trail, Grant Grove section, Kings Canyon National Park, *Shevock* 16647.

***Orthotrichum tenellum* Bruch ex Bridel**

[Orthotrichaceae]

Literature: Harpel 1980a; Harthill et al. 1979; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Long 1978; McCleary 1972; Mishler 1978; Shevock and Toren 2001; Steere 1954; Steere et al. 1954; Thomson and Ketchledge 1958; Toren 1977; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Orthotrichum coulteri* Lesquereux 1868. As *Orthotrichum cylindrocarpum* Bradshaw 1926; Kingman 1912; Lesquereux 1868; Lesquereux and James 1884; Millspaugh and Nuttall 1923; Sayre 1940; Steere 1954; Steere et al. 1954; Watson 1880. As *Orthotrichum tenellum* var. *coulteri* McCleary 1972.

Illustrations: Sharp et al. 1994; Smith 1978; Vitt 1973.

Geographic subdivisions: CW, NW, SN, SW.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris* 87190; Fresno Co.: Patterson Creek along Kings River, Sierra National Forest, *Norris* 50993; Lake Co.: north end of Bachelor Valley near Hell's Peak, *Toren* 975 (SFSU); Orange Co.: Trabuco Canyon about 3 miles east of O'Neill Park near Cleveland National Forest boundary, *Shevock* 3988; Placer Co.: Clover Valley Creek at Sierra College Road, *Norris* 81949; San Francisco Co.: Panhandle, Golden Gate Park, *Shevock* 18930; Santa Cruz Co.: San Lorenzo Park, City of Santa Cruz, *Kellman* 1832 (CAS); Sonoma Co.: South Ridge Trail above Lake Sonoma at Skaggs Spring Road, *Norris* 86911.

***Orthotrichum texanum* Sullivant & Lesquereux**

[Orthotrichaceae]

Literature: Flowers 1973; Koch 1950a; Lesquereux 1868; Lesquereux and James 1884; Steere et al. 1954. As *Orthotrichum texanum* var. *globosum* Lesquereux 1868; Lesquereux and James 1884; Steere et al. 1954; Watson 1880.

Illustrations: Flowers 1973.

Geographic subdivisions: CaR, NW.

Selected specimens: Shasta Co.: Shotgun Creek near North Fork Shotgun Creek south-southeast of Sims, Shasta-Trinity National Forest, *Norris & Hill-yard* 103890; Siskiyou Co.: Forest Road 46N65 about 2 miles north of Lake Mountain Lookout, Klamath National Forest, *Norris* 70923.

***Orthotrichum underwoodii* F. Lara, Garilleti & Mazimpaka** [Orthotrichaceae]

Literature: Garilleti et al. 2001.

Illustrations: Garilleti et al. 2001.

Geographic subdivisions: CW.

Selected specimens: Santa Clara Co.: Santa Clara Mountains, *Pringle s.n.* (NY) and Pajaro, *Underwood s.n.* (NY); Santa Cruz Co.: Felton, *Kellman* 1183 (CAS).

***Oxystegus tenuirostris* (W. J. Hooker & Taylor) A. J. E. Smith** [Pottiaceae]

Literature: As *Trichostomum tenuirostre* Lawton 1971.

Illustrations: Allen 2002; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1981; Sharp et al. 1994; Smith 1978; Zander 1993.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Madera Co.: Forest Highway 81 along Rock Creek near Rock Creek Bridge, Sierra National Forest, *Norris & Shevock* 100055; Siskiyou Co.: Klamath River at Crawford Creek, *Norris* 10483; Tulare Co.: Salmon Creek west of Rincon Trail, Kern Plateau, Sequoia National Forest, *Laeger* 1192 (CAS).

***Palustriella commutata* (Bridel) Ochya**

[Helodiaceae]

Literature: As *Hypnum commutatum* Lesquereux 1868; Watson 1880.

Illustrations: Hedenäs 1993a; Ireland 1982; Ochya 1989; Smith 1978. As *Cratoneuron commutatum* Flowers 1973; Lawton 1971. As *Cratoneuron commutatum* var. *falcatum* Lawton 1971. As *Cratoneuron falcatum* Flowers 1973.

Notes: The California material of *Palustriella* appears to be a complex array of ecological forms based on water chemistry and habitats.

Geographic subdivisions: CaR, MP, NW, SN, SNE.

Selected specimens: Inyo Co.: Robinson Lake south of Onion Valley, Inyo National Forest, *Norris* 46661 & 46664; Modoc Co.: South Fork Pine Creek, South Warner Wilderness, Modoc National Forest, *Harpel* 2312 (pers. herb.); Mono Co.: Lundy Lakes Trail along Mill Creek below Helen Lake, Inyo National Forest, *Norris* 78862; Siskiyou Co.: Jackson Creek along road between Callahan and Cecilville about 6 miles west of Callahan, Klamath National Forest, *Norris* 70504 and shore of Grass Lake along Highway 97 north of Weed, *Norris* 74482; Tulare Co.: Clover Creek off of General's Highway, Marble Fork Kaweah River, Sequoia National Park, *Shevock* 15632.

***Phascum cuspidatum* Hedwig** [Pottiaceae]

Literature: Brandege 1891; Crum and Anderson 1981; Harthill et al. 1979; Howe 1897; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Shevock and Toren 2001; Stark and Whittemore 1992; Steere et al. 1954; Toren 1977; Watson 1880. As *Tortula acaulon* Zander 1993.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978. As *Tortula acaulon* Ignatov and Ignatova 2003.

Geographical subdivisions: CaR, CW, DMoj, NW, SN, SW.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris* 87164; Contra Costa

Co.: Antioch Dunes National Wildlife Refuge, *Norris* 97052; Kern Co.: Highway 178, Kern River Canyon above first dam, Sequoia National Forest, *Norris* 80806; Lake Co.: Indian Valley Lake, *Norris* 67544; Orange Co.: Mesa Picnic Area, O'Neal Regional Park, Santa Ana Mountains, *Norris & Piippo* 82168; San Bernardino Co.: Mid-Hills Campground, Providence Mountains, Mojave National Preserve, *Norris* 81412; San Francisco Co.: Potrero Hill, *Toren* 7823 (CAS); Shasta Co.: Highway 299 at Oak Run Road, *Norris* 80343.

***Philonotis americana* (Dismier) Dismier**
[Bartramiaceae]

Literature: Holmberg 1969; Koch 1950a, 1958; Koch and Ikenberry 1954; Spjut 1971. As *Philonotis fontana* var. *americana* Flowers 1973; Strid 1974.

Illustrations: Flowers 1973; Ireland 1982; Lawton 1971.

Geographic subdivisions: CaR, NW, SN, SNE, SW.

Selected specimens: Humboldt Co.: Highway 299 at Lord Ellis Summit, *Creasy s.n.* (UC); Lake Co.: Ericson Ridge, Mt. Sanhedrin, Mendocino National Forest, *Toren* 7151 (CAS); San Bernardino Co.: Wildhorse Creek near summit of Sugarloaf Mountain, San Bernardino National Forest, *Sanders* 15027 (UC); Siskiyou Co.: Mt. Eddy, Shasta-Trinity National Forest, *Norris* 9148; Tehama Co.: near Sulfur Works, Lassen Volcanic National Park, *Koch* 1945 (UC); Tulare Co.: General's Highway, 0.9 miles above Amphitheater Point, Sequoia National Park, *Shevock* 15221.

***Philonotis caespitosa* Juratzka** [Bartramiaceae]

Literature: As *Philonotis fontana* var. *caespitosa* Flowers 1973; Strid 1974.

Illustrations: Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971. As *Philonotis fontana* var. *caespitosa* Crum and Anderson 1981.

Geographic subdivisions: SN, SNE.

Selected specimens: Fresno Co.: Cedar Grove at Granite Creek, Kings Canyon National Park, *Shevock* 13765; Tornado Meadow, Sequoia National Forest, *Norris, Shevock, & Barahona* 87997; Mono Co.: Barney Lake, Toiyabe National Forest, *Norris* 67120.

****Philonotis calcarea* (Bruch & W. P. Schimper) W. P. Schimper** [Bartramiaceae]

Illustrations: Ignatov and Ignatova 2003; Smith 1978.

Geographic subdivisions: SNE.

Selected specimens: Mono Co.: Virginia Lakes Basin at Cooney Lake, *Janeway* 7659 (UC).

***Philonotis capillaris* Lindberg** [Bartramiaceae]

Literature: Bourell 1981; Crum and Anderson 1981; Dismier 1911; Holmberg 1969; Howe 1896; Jamieson 1969; Kellman 2003; Koch 1950a;

McGrew 1976; Shevock and Toren 2001; Spjut 1971; Toren 1977; Yurky 1990, 1995.

Illustrations: Allen 2002; Crum and Anderson 1981; Lawton 1971.

Geographical subdivisions: CaR, CW, NW, SN, SNE.

Selected specimens: Humboldt Co.: Redwood Creek near junction with Highway 299, *Norris* 47072 and Avenue of the Giants above Myers Flat, *Norris* 72095; Lake Co.: Old County Road, Blue Lakes, *Toren* 7430a (CAS); Marin Co.: Lake Lagunitas, *Eastwood* 104 (CAS); Mono Co.: Harvey Monroe Hall Research Natural Area, Inyo National Forest, *Norris* 48429; San Francisco Co.: Tank Hill, *Shevock* 18918; Santa Cruz Co.: China Grade, Big Basin Redwoods State Park, *Kellman* 1318 (CAS); Sonoma Co.: Wolf Creek Road about 4 miles east of Gualala River, *Norris* 86941; Trinity Co.: East Weaver Lake, *Norris* 9398.

***Philonotis fontana* (Hedwig) Bridel**
[Bartramiaceae]

Literature: Bourell 1981; Cooke 1941; Coville 1893; Crum and Anderson 1981; Dismier 1911; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Long 1978; McGrew 1976; Showers 1982; Spjut 1971; Strid 1974; Toren 1977; Yurky 1990, 1995. As *Bartramia fontana* Lesquereux 1868; Watson 1880. As *Philonotis calcarea* forma *occidentalis* Koch 1950a.

Illustrations: Allen 2002; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Koponen et al. 1995; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, CW, MP, NW, SN, SNE, SW.

Selected specimens: Fresno Co.: Forest Road 10S66 above Bear Creek, Sierra National Forest, *Shevock & Bourell* 14014; Humboldt Co.: shore of Snow Camp Lake, *Norris* 50381; Marin Co.: Olema, *Jepson* 66 (UC); Placer Co.: North Fork Campground near Emigrant Gap, Tahoe National Forest, *Norris* 88049; Riverside Co.: Dark Canyon, San Jacinto Mountains, San Bernardino National Forest, *Harpel* 79 (pers. herb.); Santa Cruz Co.: Slippery Rock Meadow, Big Basin Redwoods State Park, *Kellman* 698 (CAS).

****Philonotis marchica* (Hedwig) Bridel**
[Bartramiaceae]

Illustrations: Ignatov and Ignatova 2003; Smith 1978.

Geographic subdivisions: CaR.

Selected specimens: Siskiyou Co.: along Ash Creek south of summit of Ash Creek Butte, High Cascade Range, *Janeway* 7633 (UC).

***Philonotis muehlenbergii* (Schwägrichen) Bridel**
[Bartramiaceae]

Literature: Yurky 1990, 1995.

Illustrations: Crum and Anderson 1981.

Geographic subdivisions: CW, GV, SN, SNE.

Selected specimens: Fresno Co.: trail between Golden Lake and Mono Pass, Sierra National Forest, *Norris* 47026; Inyo Co.: John Muir Wilderness, Inyo National Forest, slopes above Chocolate Lake west of Big Pine, *Norris* 46927, vicinity of Heart Lake between Onion Valley and Kearsarge Pass, *Norris* 46798, and Robinson Lake, *Norris* 46647; Marin Co.: Olema Valley Trail, Point Reyes National Seashore, Yurky 534 (SFSU); Sutter Co.: Philip Road near junction with Feddymont Road northwest of Roseville, *Norris* 103779; Tulare Co.: slopes above Ranger Lakes toward Silliman Pass, Roaring River Fork of Kings River, Kings Canyon National Park, *Norris* 46582.

***Philonotis tomentella* Molendo in Lorentz**

[Bartramiaceae]

Literature: Dismier 1911. As *Philonotis fontana* var. *pumila* Flowers 1973; Lawton 1971; Showers 1982.

Illustrations: Crum and Anderson 1981; Flowers 1973; Lawton 1971; Smith 1978.

Geographic subdivisions: NW, SN, SNE.

Selected specimens: Amador Co.: Devil's Lake Trail northeast of Bear River Reservoir, Eldorado National Forest, *Norris* 82680; Fresno Co.: Kearsarge Lakes, South Fork Kings River, Kings Canyon National Park, *Shevock* 14331; Lake Co.: Forest Road M-3 south of Sheetiron Mountain, Mendocino National Forest, *Shevock* 15870; Mono Co.: Harvey Monroe Hall Research Natural Area, Inyo National Forest, *Norris* 48424; Siskiyou Co.: Terrace and Upper Cliff Lakes, *Norris* 53004.

***Philonotis yezoana* Bescherelle & Cardot**

[Bartramiaceae]

Literature: Crum and Anderson 1981.

Illustrations: Czernyadjeva 1995.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Amador Co.: junction of Hidden Lake Trail and Horse Thief Spring Trail above Plasse Resort on south end of Silver Lake, Eldorado National Forest, *Norris* 82848; Humboldt Co.: Mountain View Road about 2 miles east of Kneeland, *Norris* 8612; Inyo Co.: slopes above Treasure Lake west of Big Pine, John Muir Wilderness, Inyo National Forest, *Norris* 46995; Mono Co.: Lundy Creek, Hoover Wilderness, Toiyabe National Forest, *Norris* & *Hillyard* 104152; Siskiyou Co.: near Big Duck Lake, Klamath National Forest, *Norris* 22899; Tuolumne Co.: Chewing Gum Lake on Burst Rock Trail, Emigrant Wilderness, Stanislaus National Forest, *Norris* 82985.

***Physcomitrella patens* (Hedwig) Bruch & W. P. Schimper** [Funariaceae]

Literature: Koch 1950a; Tan 1978.

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Smith 1978; Tan 1978.

Geographic subdivisions: CW.

Selected specimens: Alameda Co.: near reservoir/

pond, Mountain View Cemetery, Oakland, *Gardner s.n.* (UC) [determined by Koch].

***Physcomitrella readeri* (C. Müller Hal.) Stone & G. A. M. Scott** [Funariaceae]

Literature: As *Physcomitrella californica* Crum and Anderson 1955. As *Physcomitrella patens* var. *californica* and *P. patens* var. *readeri* Tan 1979.

Illustrations: As *Physcomitrella californica* Crum and Anderson 1955.

Geographic subdivisions: CW, GV.

Selected specimens: Alameda Co.: Lake Del Valle, *Erter* 17546 (CAS, MO, UC); Solano Co.: mudflats on Lake Chabot, *Koch* 1320 (MO, UC).

***Physcomitrium californicum* E. Britton**

[Funariaceae]

Literature: Flowers 1973; Howe 1897; Smith 1970; Toren 1977; Yurky 1990. As *Physcomitrium megalocarpum* var. *californicum* Koch 1950a; Lawton 1971.

Illustrations: Flowers 1973; Lawton 1971.

Geographic subdivisions: CaR, CW, NW, SN, SW.

Selected specimens: El Dorado Co.: Highway 49, 2.3 miles north of crossroad to Georgetown, *Tavares* 669 (UC); Humboldt Co.: Blue Slide, Van Duzen River, *Tracy* 9297 (UC); Marin Co.: Lake Lagunitas, *Eastwood* 105 (CAS); Mendocino Co.: Highway 101 at Cummings turnoff at milepost 84.91, *Norris* 21601; Riverside Co.: Mesa de Colorado, Santa Rosa Plateau, southern Santa Ana Mountains, *Shevock* 4275; San Bernardino Co.: Blue Lake, San Bernardino Mountains, *Munz* 10537 (CAS) [determined by MacFadden]; Siskiyou Co.: Highway 96 about 1 mile west of Seiad Valley, Klamath National Forest, *Norris* 58283; Tehama Co.: about 2 miles west of Dales, *Norris* 56018.

***Physcomitrium collenchymatum* Gier**

[Funariaceae]

Literature: Steen 1986.

Illustrations: Crum and Anderson 1964, 1981; Gier 1955; Ireland 1982.

Geographic subdivisions: GV, SN.

Selected specimens: Calaveras Co.: above Comanche Reservoir near Burson, *Steen* 840326–8 (CINC, DUKE, UC) [determined by Crum; Snider]; Tulare Co.: north end of Lake Kaweah near Three Rivers, *Shevock* & *York* 16903 and *Shevock* 17266.

****Physcomitrium hookeri* Hampe** [Funariaceae]

Illustrations: Crum and Anderson 1981; Flowers 1973; Lawton 1971.

Geographic subdivisions: NW, SN.

Selected specimens: Del Norte Co.: French Hill Road about 1 mile above Highway 199 southwest of Gasquet, Six Rivers National Forest, *Norris* 85031; Fresno Co.: Red Mountain east of Humphreys Station, *Shevock* & *York* 13261.

***Physcomitrium pyriforme* (Hedwig) Hampe**
[Funariaceae]

Literature: Lesquereux 1868; Watson 1880; Yurky 1995. As *Physcomitrium megalocarpum* Koch 1951e; Koch and Ikenberry 1954. As *Physcomitrium turbinatum* Bradshaw 1926; Howe 1897.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Fresno Co.: Cripe Road near junction with Peterson Mill Road, Sierra National Forest, *Shevock & York 14937*; Lake Co.: Big Valley along Soda Bay Road, *Toren 7857* (CAS); Marin Co.: Ridgecrest Boulevard, Mt. Tamalpais, *Koch 2285* (UC); Placer Co.: muddy bank, Dutch Flat, *MacFadden 9411* (MO); San Mateo Co.: Burleigh H. Murray Ranch State Park, *Whittemore 5407* (CAS); Shasta Co.: Oak Run east of Redding, *Nutting s.n.* (UC); Trinity Co.: near Hyampom, Shasta-Trinity National Forest, *Howe 1104* (UC); Tulare Co.: trail to Mosquito Lakes before junction to Eagle Lakes, Mineral King, Sequoia National Park, *Shevock & O'Brien 15919*.

***Plagiomnium cuspidatum* (Hedwig) T. Koponen**
[Mniaceae]

Literature: Kellman 2003. As *Mnium cuspidatum* Flowers 1973; Koch 1950a; Wyatt and Odrzykaski 1998.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Placer Co.: Kings Beach near shore of Lake Tahoe, Lake Tahoe Basin Management Unit, *Matson 367* (UC); Shasta Co.: Highway 299 about 24 miles east of Redding, *Norris 21596*; Siskiyou Co.: near Ducks Lake Trail near Parrots Mill Road, *Norris 22829*; Tulare Co.: Redwood Canyon, Redwood Mountain Grove, Kings Canyon National Park, *Dennis s.n.* (CAS).

****Plagiomnium ellipticum* (Bridel) T. Koponen**
[Mniaceae]

Literature: Misapplied as *Mnium affine* Cooke 1941; Holmberg 1969; Koch 1950a; Lesquereux 1868. As *Mnium rugicum* Showers 1982. As *Plagiomnium rugicum* Lawton 1971.

Illustrations: Ignatov and Ignatova 2003.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Fresno Co.: Deer Creek adjacent to Highway 180 and South Fork Kings River, Sequoia National Forest, *Shevock 12452*; Humboldt Co.: Azalea Reserve State Park, *Farr 34 & 53* (UC); Nevada Co.: Sagehen Creek about 3 miles east of UC Biological Station, Tahoe National Forest, *Norris 99446*; Mono Co.: near Green Lake, Hoover Wilderness, Toiyabe National Forest, *Norris 57247*; Siskiyou Co.: Klamath National Forest,

near Sutcliffe Creek about 13 miles northwest of Happy Camp, *Norris 83305, 83310 & 83322*, and trail to Bear Lake along Bear Creek, *Norris 83452*; Tehama Co.: Beegum Creek off of Forest Road 35 about 1.5 miles west of Rat Trap Gap, Shasta-Trinity National Forest, *Norris 56954 & 56990*; Tulare Co.: above Dorst Creek Campground, Sequoia National Park, *Shevock & Dennis 14083*.

***Plagiomnium insigne* (Mitten) T. Koponen**
[Mniaceae]

Literature: Koponen 1971; Lawton 1971; Spjut 1971; Yurky 1995. As *Mnium insigne* Bourell 1981; Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lesquereux 1868; Smith 1970.

Illustrations: Koponen 1971; Lawton 1971.

Geographic subdivisions: CW, NW, SN.

Selected specimens: Del Norte Co.: Jedediah Smith Redwoods State Park, *Norris 85080*; Humboldt Co.: near Fish Lake above Weitchpec, Six Rivers National Forest, *Norris 22225*; Lake Co.: south of Summit Lake, Mendocino National Forest, *Toren & Dearing 7210* (CAS) [determined by Wyatt]; Siskiyou Co.: road to Jackson Lake about 3.5 miles west of Callahan toward Cecilville, Klamath National Forest, *Norris 22924*; Tehama Co.: fork of Beegum Creek about 1.5 miles west of Rat Trap Gap, Shasta-Trinity National Forest, *Norris 56987*; Trinity Co.: Big Creek east of China Peak, *Norris 76829* and East Fork Road at Rich Gulch north of Helena, Shasta-Trinity National Forest, *Norris 18945*; Tulare Co.: Deer Creek area south of Lion Ridge, Greenhorn Mountains, Sequoia National Forest, *Shevock 10087*.

***Plagiomnium medium* (Bruch & W. P. Schimper) T. Koponen** [Mniaceae]

Literature: Koponen 1971; Lawton 1971; Spjut 1971. As *Mnium medium* Crum and Anderson 1981; Flowers 1973; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lesquereux 1868; Showers 1982.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Koponen 1971; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, MP, NW, SN.

Selected specimens: Humboldt Co.: Tish-Tang-a-Tang Creek near Grogans Hole, Six Rivers National Forest, *Norris 47844*; Kern Co.: north of Highway 155, 1 mile north of Tiger Flat Campground, Greenhorn Mountains, Sequoia National Forest, *Shevock 10623*; Modoc Co.: Deep Creek about 2 miles west of Cedarville-Eagleville Road, *Norris 18732*; Placer Co.: Big Tree Grove, Tahoe National Forest, *Koch 3164* (UC); Siskiyou Co.: near Cook and Green Pass about 1 mile west of White Mountain, Klamath National Forest, *Norris 50183*; Tuolumne Co.: Frazier Flat Campground along Tuolumne River off Highway 108, Stanislaus National Forest, *Norris 57123*.

***Plagiomnium rostratum* (Schrader) T. Koponen**
[Mniaceae]

Literature: Lawton 1971. As *Mnium rostratum* Harthill et al. 1979; Strid 1974. As *Mnium longirostratum* Crum and Anderson 1981; Koch 1950a.

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: NW, SN.

Selected specimens: Fresno Co.: Zumwalt Meadow, Cedar Grove, Kings Canyon National Park, *Shevock* 13778; Humboldt Co.: Oregon Creek north of Trinity Guard Station, *Norris* 50146 and South Fork of Tish-Tang-a-Tang Creek east of Hoopa, Hoopa Valley Indian Reservation, *Norris & Whittemore* 52374; Siskiyou Co.: trail along Bear Creek, *Norris* 83452 and near Bear Lake, Klamath National Forest, *Norris* 24213; Trinity Co.: Coffee Creek at trail to Boulder Creek Lakes, Shasta-Trinity National Forest, *Norris* 57446.

***Plagiomnium venustum* (Mitten) T. Koponen**
[Mniaceae]

Literature: Kellman 2003; Lawton 1971; Spjut 1971; Yurky 1990. As *Mnium venustum* Bourell 1981; Harpel 1980a; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lesquereux 1868; Toren 1977; Watson 1880.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Contra Costa Co.: Donner Canyon, Mt. Diablo State Park, *Shevock & Ertter* 20329; Del Norte Co.: Forest Road 4803, Siskiyou National Forest, *Norris* 70907; El Dorado Co.: Bear Creek Picnic Area south-southeast of Georgetown, Eldorado National Forest, *Norris & Piippo* 82339; Lake Co.: Ericson Ridge, Mt. Sanhedrin, Mendocino National Forest, *Toren* 5113 (CAS); Santa Cruz Co.: Blue Cliff, South Fork Fall Creek, *Kellman* 557 (CAS); Shasta Co.: Forest Road 39N07 along Soda Creek about 6 miles northeast of Interstate 5 south of Dunsuir, *Norris & Hillyard* 103803; Trinity Co.: Swede Creek Road about 1 mile north of intersection with road to Ironside Mountain Lookout, Shasta-Trinity National Forest, *Norris* 70711; Tulare Co.: trail to Crystal Cave near Cascade Creek, Sequoia National Park, *Shevock & Tseng* 15765.

***Plagiothecium cavifolium* (Bridel) Iwatsuki**
[Plagiotheciaceae]

Literature: McGrew 1976.

Illustrations: Ignatov et al. 1996; Ireland 1982, 1985; Iwatsuki 1970.

Geographic subdivisions: NW, SN, SNE.

Selected specimens: Del Norte Co.: Whiskey Lake, Siskiyou National Forest, *Norris* 57731; Humboldt Co.: Prairie Creek Redwoods State Park, *Norris* 70412; Mono Co.: Stanford Meadows, Harvey Monroe Hall Research Natural Area, Inyo National Forest, *Norris* 48397 and Barney Lake, Toiyabe National Forest, *Norris* 67123; Siskiyou Co.: Long Gulch Lake above Callahan, Klamath National Forest, *Norris* 57501 and Scott Camp Creek Basin, *Norris* 53079.

Plagiothecium denticulatum (Hedwig) Bruch & W. P. Schimper [Plagiotheciaceae]

Literature: Holmberg 1969; Ireland 1982, 1986; Jamieson 1969; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; McGrew 1976; Showers 1982; Spjut 1971; Yurky 1995. As *Hypnum denticulatum* Lesquereux 1868; Watson 1880.

Illustrations: Abramov and Volkova 1998; Flowers 1973; Ignatov et al. 1996; Ireland 1982, 1986; Iwatsuki 1970; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Del Norte Co.: Damnation Creek Trail, Del Norte Redwoods State Park, *Norris* 10977; Fresno Co.: Forest Road 10S66 above Bear Creek, Sierra National Forest, *Shevock & Bourell* 13997; Inyo Co.: above George Lake, Inyo National Forest, *Norris* 71467; San Mateo Co.: Pilarcitos Canyon below Lake Pilarcitos, *Steere s.n.* (UC); Siskiyou Co.: Upper Cliff Lakes, *Norris* 53033 and Big Boulder Lake west of Carrville, Shasta-Trinity National Forest, *Norris & Streimann* 74802; Tehama Co.: North Yolla Bolly Mountain, Shasta-Trinity National Forest, *Norris* 57057; Tulare Co.: trail from Panther Gap to Emerald Lake, Sequoia National Park, *Norris* 67837.

***Plagiothecium laetum* Bruch & W. P. Schimper**
[Plagiotheciaceae]

Literature: Bourell 1981; Ireland 1982, 1986; Kellman 2003; Lawton 1971; McGrew 1976; Shevock and Toren 2001; Smith 1970; Spjut 1971.

Illustrations: Ignatov et al. 1996; Ireland 1982, 1986; Lawton 1971.

Geographic subdivisions: CW, NW.

Selected specimens: Del Norte Co.: Damnation Creek Trail, Del Norte Redwoods State Park, *Norris* 46226; Humboldt Co.: Emerald Creek at junction with Redwood Creek, Redwood National Park, *Norris* 45835; Lake Co.: Bucknell Creek north of Garrett Mountain, Mendocino National Forest, *Toren & Dearing* 7414 (CAS); Mendocino Co.: along County Road 409 about 1 mile east of Highway 1 south of Fort Bragg, *Norris* 11691; San Francisco Co.: Golden Gate Park, *Shevock* 18760; Santa Cruz Co.: south of Santa Cruz, Forest of Nisene Marks State Park, *Norris* 55624.

***Plagiothecium piliferum* (Swartz ex C. J. Hartman) Bruch & W. P. Schimper**
[Plagiotheciaceae]

Literature: Ireland 1986; Spjut 1971.

Illustrations: Ireland 1985; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, NW.

Selected specimens: Del Norte Co.: South Siskiyou Fork below Prescott Cabin, *Norris* 47920; Humboldt Co.: near French Camp, *Norris* 24311

and Forest Road 10N02 at head of Mill Creek, *Norris* 70581; Shasta Co.: Soda Creek Road, 3 miles northeast of Interstate 5 near Dunsmuir, *Norris* 84785; Siskiyou Co.: near Sutcliffe Falls about 14 miles northwest of Happy Camp, Klamath National Forest, *Norris* 83319.

***Platydictya jungermannioides* (Bridel) H. Crum**
[Hypnaceae]

Literature: Kellman 2003; Lawton 1971; Showers 1982.

Illustrations: Flowers 1973; Ignatov et al. 1996; Ireland 1982; Lawton 1971; Ochyra 1998a; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN, SNE.

Selected specimens: Fresno Co.: Redwood Creek, Windy Gulch Redwood Grove, Sequoia National Forest, *Norris, Shevock, & York* 87961 and Dinkey Lakes Trailhead, Sierra National Forest, *York* 1128 (CAS, UC); Inyo Co.: Little Lakes Creek near Long Lake, *Norris* 79013; Mono Co.: Lundy Lakes Trail, Inyo National Forest, *Norris* 78902; Santa Cruz Co.: Wilder Ranch State Park, *Kellman* 817 (CAS) and Santa Cruz City, *Kellman* 1093 (CAS); Shasta Co.: Squaw Valley Creek southwest of McCloud, Shasta-Trinity National Forest, *Norris & Hillyard* 104294; Siskiyou Co.: trail from Big Flat to Yellow Rose Mine, *Norris* 9124 and Salmon River near Big Flat, *Norris* 9168, Jaynes Creek northwest of Klamath River, *Norris* 48702; Tulare Co.: Kaweah River near Atwell Mills Campground west of Mineral King, Sequoia National Park, *Norris* 46451 & 46480 and Squirrel Creek off of County Road 372 about 1 mile below Oriole Lake, *Shevock* 17646.

***Platyhypnidium riparioides* (Hedwig) Dixon**
[Brachytheciaceae]

Literature: Kellman 2003; Koch 1950a. As *Eurhynchium riparioides* Harthill et al. 1979; Ireland 1982; Jamieson 1969; Lawton 1971; McGrew 1976. As *Hypnum rusciforme* Watson 1880. As *Rhynchostegium rusciforme* Howe 1897; Lesquereux 1868.

Illustrations: Ignatov 1998; Ireland 1982; Lawton 1971.

Geographic subdivisions: CaR, CW, NW.

Selected specimens: Butte Co.: Martin Creek near Brush Creek about 10 miles east of Oroville, *Dillingham* 804 (UC); Del Norte Co.: Prairie Creek Trail north of Hunnewell-Donald Grove, *Jamieson* 69 (UC); Humboldt Co.: Redwood Valley Road about 0.65 mile from Highway 299, *Farr* 77 (UC) [determined by Jamieson] and Haul Road on south margin of Prairie Creek, Prairie Creek Redwoods State Park, *Norris* 71735 & *Jamieson* 69 (UC); Lake Co.: Alder Creek, Cobb Mountain, *Toren & Dearing* 7096 (CAS); Santa Cruz Co.: Barrel Mill Creek, Ben Lomond Mountain, *Kellman* 679 (CAS).

***Pleuridium acuminatum* Lindberg** [Ditrichaceae]

Literature: Kellman 2003; Koch 1950a; Shevock and Toren 2001; Yip 2000, 2002; Yurky 1995. As *Pleuridium bakeri* Cardot and Thériot 1904. As *Pleuridium bakeri* var. *elongatum* Cardot and Thériot 1904. As *Pleuridium bolanderi* Bourell 1981; Brandegee 1891; Harpel 1980a; Harthill et al. 1979; Kingman 1912; Koch 1950a; Koch and Ikenberry 1954; Lesquereux and James 1884; Mishler 1978; Steere et al. 1954; Toren 1977. As *Pleuridium californicum* Grout 1928–1940; Harthill et al. 1979; Koch 1950a; Stark and Whitemore 1992. As *Pleuridium stramineum* Austin 1877c; Jamieson 1969; Smith 1970.

Illustrations: Smith 1978; Yip 2000.

Geographic subdivisions: CW, GV, NW, SN, SW.

Selected specimens: Contra Costa Co.: Mt. Diablo State Park, *Norris* 100537; Fresno Co.: Cripe Road, 0.65 miles from junction with Peterson Mill Road, Sierra National Forest, *Shevock & York* 14938 (determined by Yip); Lake Co.: Hidden Valley north of Middletown, *Toren & Dearing* 7578 (CAS) [determined by Yip]; Mendocino Co.: County Road 409 about 1 mile east of Highway 1 south of Fort Bragg, *Norris* 11738, 11747 & 11770 (determined by Yip); Riverside Co.: Forest Road 4S05, San Jacinto Mountains, San Bernardino National Forest, *Harpel* 976 (pers. herb.); Santa Cruz Co.: near Ben Lomond, *Kellman* 190 (CAS); Trinity Co.: near Denny, *Norris* 10723 (determined by Yip).

***Pleuridium subulatum* (Hedwig) Rabenhorst**
[Ditrichaceae]

Literature: Bradshaw 1926; Crum and Anderson 1981; Kellman 2003; Lawton 1971; Lesquereux 1868; Shevock and Toren 2001; Sigal 1975; Watson 1880; Yip 2000, 2002; Yurky 1990, 1995. As *Pleuridium alternifolium* var. *howei* Renauld and Cardot 1893.

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978; Yip 2000.

Geographic subdivisions: CaR, CW, GV, NW, SN.

Selected specimens: Butte Co.: Neal Road south of Chico to Paradise about 0.5 mile east of Highway 99, *Norris* 10611a (determined by Yip); Del Norte Co.: French Hill, Six Rivers National Forest, *Harpel* 3166 (pers. herb.); Fresno Co.: Sycamore Flat Campground, Pine Flat Reservoir, Sierra National Forest, *Norris* 50970; Lake Co.: Highway 175 at Loch Lomond along edge of swamp near Hobergs, *Toren* 7444 (CAS) [determined by Yip]; Marin Co.: Temelpa Trail, Mt. Tamalpais State Park, *Yurky* 537 (SFSU); Santa Cruz Co.: Henry Cowell State Park, *Kellman* 594 (CAS).

***Pogonatum contortum* (Menzies ex Bridel) Lesquereux** [Polytrichaceae]

Literature: Koch 1950a; Lawton 1971; Lesquereux 1868; Watson 1880. As *Pogonatum laterale* Holmberg 1969; Jamieson 1969.

Illustrations: Lawton 1971.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: Highway 299, Jedediah Smith Redwoods State Park, *Norris* 85073, trail between Requa and False Klamath Cove, Redwood National Park, *Norris* 70375; Humboldt Co.: Prairie Creek Redwoods State Park, *Norris* 7930 and 2 miles north of Pollywog Butte, *Norris* 23417 and *MacFadden* 22227 (MO), and north of Orick on Fern Canyon Road about 0.1 mile north of Fern Canyon, *Mueller* 6715 (MO) [determined by Pursell].

****Pohlia andalusica* (Höhnelt) Brotherus**

[Mniaceae]

Illustrations: Ignatov and Ignatova 2003; Ireland 1982; Shaw 1981c.

Geographic subdivisions: CW, NW.

Selected specimens: Del Norte Co.: north side Smith River about 1 mile west of Gasquet, Six Rivers National Forest, *Norris* 70344; Santa Cruz Co.: Mill Street Dam, San Lorenzo River, *Kellman* 2918 (CAS).

***Pohlia annotina* (Hedwig) Lindberg** [Mniaceae]

Literature: Crum and Anderson 1981; Flowers 1973; Harthill et al. 1979; Holmberg 1969; Koch 1950a, 1951f; Lawton 1971; McGrew 1976; Shaw 1981c; Showers 1982; Spjut 1971; Strid 1974; Torren 1977.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Shaw 1981c.

Geographic subdivisions: CaR, MP, NW.

Selected specimens: Modoc Co.: Patterson Lake, South Warner Wilderness, Modoc National Forest, *Harpel* 2283 (pers. herb.); Siskiyou Co.: upper reaches of Scott Camp Creek Basin, *Norris* 53072.

***Pohlia bolanderi* (Lesquereux) Brotherus**

[Mniaceae]

Literature: Shaw 1982. As *Bryum bolanderi* Lesquereux 1868. As *Webera bolanderi* Lesquereux and James 1884.

Illustrations: Shaw 1982.

Geographic subdivisions: NW, SN, SNE, SW.

Selected specimens: Fresno Co.: Dinkey Lake, Dinkey Lake Wilderness, Sierra National Forest, *Shevock & York* 13894 (determined by Shaw); Inyo Co.: Chocolate Lake west of Big Pine, John Muir Wilderness, Inyo National Forest, *Norris* 46865 (determined by Shaw); Mono Co.: Lee Vining Creek at Lee Vining Campground, *Norris* 48374 (determined by Shaw); Siskiyou Co.: English Lake, Klamath National Forest, *Spjut* 1562 (UC); Trinity Co.: near Browns Meadow, *Norris* 23139 (determined by Shaw); Tulare Co.: Slate Mountain Botanical Area, headwaters of the Middle Fork Tule River, Sequoia National Forest, *Shevock* 15678 & 15690 and First Mosquito Lake, Mineral King, Sequoia National Park, *Shevock & O'Brien* 15952 (determined by Shaw); Ventura Co.: summit road

near Mt. Pinos about 1 mile below Chula Vista Campground, Los Padres National Forest, *Laeger* 1719 (CAS).

****Pohlia bolanderi* (Lesquereux) Brotherus var. *seriata* Shaw** [Mniaceae]

Illustrations: Shaw 1982.

Geographic subdivisions: NW, SN.

Selected specimens: Siskiyou Co.: between Waterdog and Russian Lakes, Klamath National Forest, *McGrew* 363 (UC) [confirmed by Spence]; Tuolumne Co.: below Olmstead Point, Tioga Road, Yosemite National Park, *Kellman* 552 (CAS).

***Pohlia camptotrachela* (Renauld & Cardot)**

Brotherus [Mniaceae]

Literature: Koch 1958; Koch and Ikenberry 1954; Renauld and Cardot 1888; Shaw 1981c.

Illustrations: Ignatov and Ignatova 2003; Shaw 1981c.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Fresno Co.: Highway 180 about 2.5 miles north of Indian Basin, Sequoia National Forest, *Shevock & York* 17137 and between Crown Creek and Blue Canyon, Kings Canyon National Park, *Shevock & York* 14136 (determined by Shaw); Humboldt Co.: junction of Thomas Road and Salmon Creek Road, *Nomura & Kim* 103 (UC) and Tish-Tang-a-Tang Creek near Grogans Hole, Six Rivers National Forest, *Norris* 47832 (determined by Shaw); Inyo Co.: Baxter Pass Trail, Big-horn Sheep Zoological Area, John Muir Wilderness, Inyo National Forest, *Shevock* 16617; Madera Co.: Norris Creek along Norris Lake Trail, Sierra National Forest, *Shevock & Kellman* 19696 (determined by Shaw); Mariposa Co.: Summit Road about 2 miles north of Fish Camp, Sierra National Forest, *Norris* 85363; Placer Co.: near Haig Tree, Tahoe Redwood Grove, Tahoe National Forest, *Koch* 3155 (UC) [determined by Shaw]; Siskiyou Co.: near Doe Flat, *Norris* 47931 (determined by Shaw); Tulare Co.: trail from Silliman Pass to Lodgepole, Sequoia National Park, *Norris* 46526; Tuolumne Co.: near Herring Creek Reservoir, Stanislaus National Forest, *Norris* 100399.

***Pohlia cardotii* (Renauld in Renauld & Cardot)**

Brotherus [Mniaceae]

Literature: Shaw 1982.

Illustrations: Lawton 1971; Shaw 1982.

Geographic subdivisions: SN, SNE.

Selected specimens: Inyo Co.: vicinity of Heart Lake on trail from Onion Valley to Kearsarge Pass, John Muir Wilderness, Inyo National Forest, *Norris* 46817; Tulare Co.: slopes above Ranger Lakes at Silliman Pass, Kings Canyon National Park, *Norris* 46539 (determined by Shaw).

***Pohlia cruda* (Hedwig) Lindberg** [Mniaceae]

Literature: Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Howe 1896; Jamieson 1969; Koch 1950a,

1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Long 1978; McGrew 1976; Shaw 1982; Showers 1982; Strid 1974; Yurky 1990, 1995. As *Bryum crudum* Lesquereux 1868; Watson 1880. As *Webera cruda* Lesquereux and James 1884.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Ochyra 1998a; Shaw 1982; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, MP, NW, SN, SNE, SW.

Selected specimens: Del Norte Co.: Mill Creek, Jedediah Smith Redwood State Park, *Norris* 23110 (determined by Shaw); Inyo Co.: east of Dragon Peak and north of Golden Trout Lake, John Muir Wilderness, Inyo National Forest, *Norris* 46720 (determined by Shaw); Mariposa Co.: Half Moon Meadow on trail to Ten Lakes, Yosemite National Park, *Shevock, Wilken, & Fritzke* 18495 (determined by Shaw); Modoc Co.: about 16 miles east of Medicine Lake on road to Beeler Reservoir, *Norris* 22499 (determined by Shaw); Riverside Co.: trail to Mt. San Jacinto, San Jacinto State Park, *Harpel* 1048 (pers. herb.); Trinity Co.: above Terrace and Upper Cliff Lakes, *Norris* 53011; Tulare Co.: road to Mineral King near Silver City, Sequoia National Park, *Shevock* 17657 (determined by Shaw).

***Pohlia drummondii* (C. Müller Hal.) Andrews in Grout** [Mniaceae]

Literature: Flowers 1973; Koch 1950a, 1958; Koch and Ikenberry 1954; Lawton 1971; McGrew 1976; Shaw 1981c, 1982; Showers 1982; Strid 1974. As *Bryum commutatum* Watson 1880. As *Bryum nudicaule* Lesquereux 1868; Watson 1880. As *Webera commutata* Lesquereux and James 1884. As *Webera nudicaulis* Lesquereux and James 1884.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971; Shaw 1981c.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Fresno Co.: Baxter Lake, Kings Canyon National Park, *Shevock & York* 16550 (determined by Shaw); Inyo Co.: Dingleberry Lake above Lake Sabrina, John Muir Wilderness, Inyo National Forest, *Raven s.n.* (CAS) [determined by Shaw]; Siskiyou Co.: Squaw Valley Creek, Mount Shasta, Shasta-Trinity National Forest, *W. B. Cooke* 15756a-c (UC) [determined by Shaw]; Tulare Co.: Slate Mountain, Sequoia National Forest, *Shevock* 15680.

***Pohlia elongata* Hedwig** [Mniaceae]

Literature: Flowers 1973; Harpel 1980a; Harthill et al. 1979; Long 1978; Shaw 1982. As *Bryum polymorphum* Lesquereux 1868. As *Pohlia acuminata* Koch 1950a. As *Pohlia elongata* var. *greenii* Shaw 1982. As *Webera polymorpha* Lesquereux and James 1884.

Illustrations: Allen 2002; Crum and Anderson

1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Shaw 1982; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: SN, SW.

Selected specimens: Riverside Co.: Cedar Springs, Santa Rosa Mountains, *Harpel* 2348a (pers. herb.); Tulare Co.: Forest Road 14S11 just east of bridge crossing of Big Meadows Creek, Sequoia National Forest, *Shevock & York* 13680 and Marble Falls Trail above Potwisha Campground, Sequoia National Park, *Shevock* 12936 (confirmed by Shaw); Unspecified county: *Bolander* 347 & 367 (NY).

***Pohlia filum* (W. P. Schimper) Mårtensson** [Mniaceae]

Literature: As *Pohlia schleicheri* Toren 1977. **Illustrations:** Ignatov and Ignatova 2003; Shaw 1981c.

Notes: The original published source for this taxon as occurring in California has been determined to be a different *Pohlia* species.

Geographic subdivisions: CaR, GV, NW.

Selected specimens: Shasta Co.: Shasta College turnoff, Interstate 5 north of Redding, *Norris* 57777; Siskiyou Co.: from Cracker Meadows to Young Valley, *Norris & Ignatov* 74704.

****Pohlia lescuriana* (Sullivant) Ochi** [Mniaceae]

Illustrations: Ignatov and Ignatova 2003; Ireland 1982; Shaw 1982.

Geographic subdivisions: CaR, GV, NW.

Selected specimens: Del Norte Co.: Coastal Trail between Regua and False Klamath Cove, Redwood National Park, *Norris* 24001; Humboldt Co.: near Round Prairie about 3 miles north of Highway 299 on Wiregrass Ridge, *Norris* 52911 (determined by Shaw) and near Coyote Peak on Bald Hills Road, *Norris* 22343; Tehama Co.: Battle Creek southeast of Manton, *Norris* 21320.

***Pohlia longibracteata* Brotherus in Röhl** [Mniaceae]

Literature: Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a; Lawton 1971; Shaw 1982; Steere et al. 1954; Thomson and Ketchledge 1958; Yurky 1990, 1995. As *Mniobryum longibracteatum* Koch and Ikenberry 1954.

Illustrations: Lawton 1971; Shaw 1982.

Geographic subdivisions: CW, NW, SN.

Selected specimens: Del Norte Co.: Damnation Creek, Del Norte Redwood State Park, *Norris & Taranto* 10972; Humboldt Co.: about 2 miles north of Redwood Valley, *Norris* 21203 (determined by Shaw); Marin Co.: north of Mt. Tamalpais, *Toren* 315 (SFSU); Mendocino Co.: Highway 1 near Rockport at milepost 101, *Norris* 8552 (determined by Shaw); Nevada Co.: Washington Creek, 4.1 miles from Highway 20, Tahoe National Forest, *Shevock & Toren* 20734 (confirmed by Shaw); Santa Cruz Co.: near Porter Picnic area, 2.8 miles north of Aptos, Forest of Nisene Marks State Park, *D. W.*

Taylor 14662 (UC) and Wilder Creek, *Kellman 827* (CAS).

***Pohlia ludwigii* (Sprengel ex Schwägrichen)
Brotherus [Mniaceae]**

Literature: Koch 1950a; Lesquereux 1868; Spjut 1971. As *Bryum bigelovii* Lesquereux and James 1884; Shaw 1982; Sullivant 1856.

Illustrations: Ignatov and Ignatova 2003; Lawton 1971; Shaw 1982.

Notes: This species for California is based on the type of *Bryum bigelovii* Sullivant (1856).

Geographic subdivisions: SN.

Selected specimens: Reported from near Sonora (Tuolumne County) and mapped for the Sierra Nevada in Shaw (1982). However, we have not located a California specimen of this species during our herbarium search in California herbaria.

***Pohlia nutans* (Hedwig) Lindberg [Mniaceae]**

Literature: Bradshaw 1926; Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Kellman 2003; Kingman 1912; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; McGrew 1976; Shaw 1982; Shevock and Toren 2001; Showers 1982; Spjut 1971; Strid 1974; Yurky 1990, 1995. As *Bryum nutans* var. *bicolor* Lesquereux 1868; Watson 1880.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Ochrya 1998a; Sharp et al. 1994; Shaw 1982; Smith 1978.

Geographic subdivisions: CaR, CW, NW, SN, SNE.

Selected specimens: Alameda Co.: near Claremont Hotel, Berkeley, *Morse 26* (UC) [determined by Shaw]; Fresno Co.: between Crown Creek and Blue Canyon, Kings Canyon National Park, *Shevock & York 14142* (determined by Shaw); Lake Co.: south shore of Clear Lake at Sulfur Bank Mine, *Toren & Dearing 7278* (CAS); Mendocino Co.: Pgymy Cypress Forest along Summers Lane near Highway 20 and Fort Bragg, *Norris 11768*; Mono Co.: near Lake Mary, Mammoth Lakes region, Inyo National Forest, *Shevock & Nelson 13787* (determined by Shaw); Nevada Co.: Sagehen Creek Biological Station, Tahoe National Forest, *Tavares 1963* (UC) [determined by Shaw]; Siskiyou Co.: trail to Paradise Lake about 1 mile from Marble Valley Guard Station, *Spjut 1140* (UC); Tulare Co.: Slate Mountain Botanical Area, Sequoia National Forest, *Shevock 15680* (determined by Shaw).

***Pohlia obtusifolia* (Villars ex Bridel) L. Koch
[Mniaceae]**

Literature: Koch 1950a, 1958; McGrew 1976; Shaw 1982. As *Bryum cucullatum* Lesquereux 1868; Watson 1880. As *Webera cucullata* Lesquereux and James 1884.

Illustrations: Lawton 1971; Shaw 1982; Smith 1978.

Geographic subdivisions: SN, SNE.

Selected specimens: Fresno Co.: Highway 180 near Yucca Point Trail, Sequoia National Forest, *Shevock 12469* and near Taaboose Pass, Kings Canyon National Park, *York 1520* (UC); Inyo Co.: north of Mt. Powell near Lake Sabrina, Outlet Creek, John Muir Wilderness, Inyo National Forest, *Laeger 46a* (CAS, DUKE) [determined by Shaw]; Kern Co.: Cache Creek east of Horse Canyon north of Tehachapi, *Shevock & Hare 14908*; Mono Co.: Koenig Lake near Leavitt Lake, east of Sonora Pass, Toiyabe National Forest, *Spjut, Norris, & J. Koponen 6260* (UC).

***Pohlia pacifica* A. J. Shaw [Mniaceae]**

Literature: Kellman 2003; Shaw 1982.

Illustrations: Shaw 1982.

Geographic subdivisions: CW, NW.

Selected specimens: Del Norte Co.: Del Norte Redwoods State Park, *Shaw 4173* (MICH) and Prairie Creek Redwoods State Park, *Norris & Piippo 82472*; Lake Co.: between Summit Lake and Smokehouse Creek, Mendocino National Forest, *Toren & Dearing 7651* (CAS) [confirmed by Shaw]; Marin Co.: Chimney Peak Trailhead, *Robertson 1834* (UC); Santa Cruz Co.: Big Creek in Swanton, *Kellman 1906* (CAS) and Ben Lomond, San Lorenzo River, *Kellman 1164* (CAS).

***Pohlia prolifera* (Kindberg) Brotherus
[Mniaceae]**

Literature: Crum and Anderson 1981; Shaw 1981c, 1982; Showers 1982.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Shaw 1981c, 1982; Smith 1978.

Geographic subdivisions: CaR, MP, SN, SNE.

Selected specimens: Inyo Co.: Taaboose Creek Trail, John Muir Wilderness, Inyo National Forest, *Shevock 13881* (determined by Shaw); Modoc Co.: Patterson Lake, South Warner Wilderness, Modoc National Forest, *Harpel 2284* (pers. herb.); Siskiyou Co.: Sisson Southern Trail, Mt. Shasta, *Cooke 15657c* (UC) [determined by Shaw].

***Pohlia tundrae* A. J. Shaw [Mniaceae]**

Literature: Shaw 1981a, 1981c, 1982.

Illustrations: Shaw 1981a, 1981c, 1982.

Geographic subdivisions: NW, SN, SNE.

Selected specimens: Fresno Co.: South Fork Tamarack Creek, Highway 168 between Shaver Lake and Huntington Lake, Sierra National Forest, *Norris 99908*; Inyo Co.: above Robinson Lake south of Onion Valley, Inyo National Forest, *Norris 46638*; Siskiyou Co.: Bingham Lake, *McGrew 637* (UC); Tulare Co.: Primrose Lake, Sequoia National Park, *J.T. Howell s.n.* (CAS) and Bakeoven Meadows, Inyo National Forest, *J.T. Howell s.n.* (CAS) [determined by Shaw].

***Pohlia wahlenbergii* (Weber & D. Mohr)
Andrews in Grout [Mniaceae]**

Literature: Bourell 1981; Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Long 1978; McGrew 1976; Mishler 1978; Shaw 1981f, 1982; Shevock and Toren 2001; Showers 1982; Spjut 1971; Toren 1977. As *Bryum albicans* Brandegee 1891; Lesquereux 1868; Watson 1880. As *Mniobryum albicans* Kingman 1912. As *Mniobryum wahlenbergii* Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954. As *Webera albicans* Lesquereux and James 1884; Moxley 1928.

Illustrations: Allen 2002; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Koponen et al. 1995; Lawton 1971; Sharp et al. 1994; Shaw 1982; Smith 1978.

Geographic subdivisions: CaR, CW, MP, NW, SN, SNE, SW.

Selected specimens: Fresno Co.: near junction between Dinkey and Mystery Lake, Dinkey Lakes Wilderness, Sierra National Forest, *Shevock & York 13929* (confirmed by Shaw); Humboldt Co.: along Dyerville to Mattole Road about 2 miles north of Panther Gap, *Norris 24129* (determined by Shaw); Modoc Co.: Big Valley Mountains, *Baker & Nutting s.n.* (UC) [confirmed by Shaw]; Monterey Co.: town of Arroyo Seco along Highway 101, *Norris 48520* (determined by Shaw); Nevada Co.: Washington Road, 2.7 miles from Highway 20, Tahoe National Forest, *Shevock & Toren 20714*; San Francisco Co.: San Francisco, *Rattan s.n.* (UC) [determined by Shaw]; Santa Barbara Co.: La Jolla Vieja Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock & Rodriguez 20866* (determined by Shaw); Tulare Co.: Watchtower Loop Trail to Heather Lake, Sequoia National Park, *Shevock 16456* (determined by Shaw).

***Polytrichastrum alpinum* (Hedwig) G. L. Smith
[Polytrichaceae]**

Literature: Kellman 2003; McGrew 1976; Shevock and Toren 2001. As *Pogonatum alpinum* Cooke 1941; Flowers 1973; Holmberg 1969; Howe 1897; Ireland 1982; Koch 1950a, 1958; Lawton 1971; Lesquereux 1868; Showers 1982; Spjut 1971. As *Pogonatum alpinum* var. *brevifolium* Watson 1880. **Illustrations:** Flowers 1973; Ignatov and Smith Merrill 1995; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Ochya 1998a; Sharp et al. 1994; Smith 1971; Smith 1978.

Geographic subdivisions: CaR, CW, MP, NW, SN, SNE.

Selected specimens: Del Norte Co.: Smith River along Highway 199 about 9 miles east of junction with Highway 1, Six Rivers National Forest, *Norris 85029*; Inyo Co.: slopes above George Lake west of Bishop, John Muir Wilderness, Inyo National Forest, *Norris 71448*; Modoc Co.: Highway 89 at Bear Creek, *Norris 77949*; San Francisco Co.: Mt. Davidson, *Toren 7764* (CAS); Santa Cruz Co.:

West Berry Creek, Big Basin Redwoods State Park, *Kellman 2487* (CAS); Shasta Co.: Summit Lake, Highway 89, Lassen Volcanic National Park, *Duell 2079* (UC); Trinity Co.: Rush Creek below Rush Creek Lakes, Trinity Alps Wilderness, Shasta-Trinity National Forest, *Norris 85411*.

***Polytrichum commune* Hedwig [Polytrichaceae]**

Literature: Bradshaw 1926; Flowers 1973; Ireland 1982; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; McGrew 1976; Showers 1982; Spjut 1971.

Illustrations: Abramov and Volkova 1998; Flowers 1973; Ignatov and Ignatova 2003; Ignatov and Smith Merrill 1995; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1971, 1978.

Notes: The Humboldt County plants in coastal prairie areas are up to 1 foot tall.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Calaveras Co.: Highway 4 at road to Spicer Reservoir, Stanislaus National Forest, *Norris 77177*; Fresno Co.: east slope Bald Mountain, Sierra National Forest, *Shevock 10992*; Humboldt Co.: Christmas Prairie, *Bonstell s.n.* (UC); Mendocino Co.: Pygmy Cypress Forest along Caspar Little Lake Road about 6 miles east of Highway 1, *Norris & Piippo 82501*; Nevada Co.: Pacific Crest Trail south of Interstate 80, Donner Summit, Tahoe National Forest, *Whitemore 4158* (MO); Siskiyou Co.: near Doe Flat, *Norris 47938*; Tulare Co.: edge of Heather Lake, Sequoia National Park, *Shevock 16489*; Tuolumne Co.: Wheat's Meadow Trail near Whittakers, Dardanelles, Stanislaus National Forest, *Somer 86* (MO).

***Polytrichum formosum* Hedwig [Polytrichaceae]**

Literature: Koch 1950a; McGrew 1976; Showers 1982.

Illustrations: Abramov and Volkova 1998; Ignatov and Smith Merrill 1995; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1971, 1978. As *Polytrichastrum formosum* Ignatov and Ignatova 2003.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Alpine Co.: Highway 89 at Hope Valley, *Norris 48477*; Butte Co.: North Table Mountain, northeast of Cherokee Road, *Janeway 5568* (MO) [determined by Whitemore]; Inyo Co.: Horton Lakes area, Inyo National Forest, *Harpel 2369* (pers. herb.); Mono Co.: Gardisky Lake west of Lee Vining, Inyo National Forest, *Norris 104223*; Siskiyou Co.: Duck Lakes trail near Parrott's Mill Road, *Norris 22818* and Pacific Crest Trail about 30 miles northeast of Sneed Valley, *G. Allen 712* (MO) [determined by Allen]; Tulare Co.: Big Meadows near Ranger Station, Sequoia National Forest, *Shevock 13670*.

***Polytrichum juniperinum* Hedwig [Polytrichaceae]**

Literature: Bourell 1981; Cooke 1941; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Ireland 1982; Jamieson 1969; Kellman 2003; Koch 1950a,

1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Long 1978; McGrew 1976; Shevock and Toren 2001; Showers 1982; Smith 1970; Spjut 1971; Strid 1974; Sullivant 1856; Toren 1977; Watson 1880; Yurky 1990, 1995.

Illustrations: Flowers 1973; Ignatov and Ignatova 2003; Ignatov and Smith Merrill 1995; Ireland 1982; Lawton 1971; Ochrya 1998a; Sharp et al. 1994; Smith 1971, 1978.

Geographic subdivisions: CaR, CW, MP, NW, SN, SNE, SW.

Selected specimens: Del Norte Co.: Forest Road 4803, Siskiyou National Forest, *Norris* 70904; San Francisco Co.: Glen Canyon, San Miguel Hills, *Shevock* 18882 & 18892; Santa Barbara Co.: Water Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock & Rodriguez* 20808; Santa Cruz Co.: Highway 9 about 1.5 miles north of Boulder Creek, *Norris* 55572; Siskiyou Co.: Soda Creek Road about 4 miles northeast of Interstate 5 near Dunsmuir, Shasta-Trinity National Forest, *Norris* 84810; Sonoma Co.: South Ridge Trail above Lake Sonoma at Skaggs Springs Road, *Norris* 86916; Tulare Co.: Grapevine Grade along County Road M-15, between White River and California Hot Springs, *Shevock* 6766.

***Polytrichum longisetum* Swartz ex Bridel**

[Polytrichaceae]

Literature: Ireland 1982. As *Polytrichum gracile* Flowers 1973; Koch 1950a. As *Polytrichastrum longisetum* Lawton 1971.

Illustrations: Abramov and Volkova 1998; Flowers 1973; Ignatov and Smith Merrill 1995; Ireland 1982; Lawton 1971; Smith 1971. As *Polytrichastrum longisetum* Ignatov and Ignatova 2003.

Geographic subdivisions: MP, NW, SN, SNE.

Selected specimens: Fresno Co.: west of Palisade Crest, Glacier Lake, Kings Canyon National Park, *DeDecker* 2796 (CAS); Inyo Co.: above Robinson Lake south of Onion Valley, Inyo National Forest, *Norris* 46635; Modoc Co.: Alcohol Crater Rim, Modoc National Forest, *Harpel* 16319 (pers. herb.); Siskiyou Co.: ridges south of Cyclone Gap, *Holmberg* 878 (UC); Tulare Co.: Crabtree Meadows, west of Mt. Whitney, Sequoia National Park, *Raven s.n.* (CAS).

***Polytrichum piliferum* Hedwig** [Polytrichaceae]

Literature: Bourell 1981; Coville 1893; Flowers 1973; Harthill et al. 1979; Holmberg 1969; Ireland 1982; Kellman 2003; Kingman 1912; Koch 1950a, 1958; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; McGrew 1976; Mishler 1978; Shevock and Toren 2001; Showers 1982; Strid 1974; Sullivant 1856; Toren 1977; Watson 1880; Yurky 1990, 1995.

Illustrations: Flowers 1973; Ignatov and Ignatova 2003; Ignatov and Smith Merrill 1995; Ireland 1982; Lawton 1971; Ochrya 1998a; Smith 1978.

Geographic subdivisions: CaR, CW, MP, SN, SNE, SW.

Selected specimens: Del Norte Co.: along Oregon Mountain Road near Highway 199 about 6 miles south of the Oregon border, *Norris* 9869; Fresno Co.: near Boyden Cave, Monarch Wilderness, Sequoia National Forest, *Shevock & York* 12293; Lake Co.: Bachelor Valley near Hell's Peak, *Toren & Dearing* 6856 (CAS); Mono Co.: above Second Tyee Lake south of Mammoth Lakes, Inyo National Forest, *Norris* 86812; Monterey Co.: bluffs at the Pinnacles, Hunter-Liggett Military Reservation, *Norris* 87294; Tehama Co.: Highway 36 east of Red Bluff at Seven Mile Creek, *Norris* 21303.

***Polytrichum sexangulare* Flörke ex Bridel**

[Polytrichaceae]

Literature: Showers 1982.

Illustrations: Ignatov and Smith Merrill 1995; Lawton 1971; Smith 1971. As *Polytrichastrum sexangulare* Ignatov and Ignatova 2003.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Fresno Co.: slopes from Mono Pass to Golden Lake, *Norris* 47032; Inyo Co.: slopes above Chocolate Lake west of Big Pine, John Muir Wilderness, Inyo National Forest, *Norris* 46872 & 46875 and slopes above Treasure Lake, Inyo National Forest, *Norris* 46966; Shasta Co.: near Soda Lake, Lassen Volcanic National Park, *Showers* 837 (UC); Tulare Co.: summit plateau of Table Mountain, Sequoia National Park, *Laeger* 162 (CAS, UC).

****Polytrichum strictum* Menzies ex Bridel**

[Polytrichaceae]

Illustrations: Ignatov and Ignatova 2003; Smith 1978.

Geographic subdivisions: SN.

Selected specimens: Nevada Co.: about 0.5 mile northeast of Bowman Lake, Tahoe National Forest, *Ahart* 10612 (UC).

***Porotrichum bigelovii* (Sullivant) Kindberg**

[Neckeraceae]

Literature: Bourell 1981; Frantz and Cordone 1967; Holmberg 1969; Jamieson 1969; Showers 1982; Yurky 1990, 1995. As *Hypnum bigelovii* Lesquereux 1868; Sullivant 1856; Watson 1880. As *Porothamnium bigelovii* Bradshaw 1926; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Smith 1970; Spjut 1971; Steere et al. 1954; Thomson and Ketchledge 1958. **Illustrations:** Lawton 1971; Schofield and Thompson 1966; Sullivant 1856.

Geographic subdivisions: CaR, CW, NW, SN, SW.

Selected specimens: Del Norte Co.: Highway 199 about 9 miles east of junction with Highway 101, Six Rivers National Forest, *Norris* 84993; El Dorado Co.: Bear Creek Picnic Area southeast of Georgetown, Eldorado National Forest, *Norris & Piippo* 82323; Lake Co.: Alder Creek, Cobb Mountain, *Toren & Dearing* 7087 (CAS); Mendocino

Co.: seaward bluffs near Ranger Station, Sinkyone Wilderness State Park, *Norris* 71743; San Francisco Co.: Delaveaga Dell, AIDS Memorial Grove, Golden Gate Park, *Hermann* 17451 and *Shevock* 19526; Santa Barbara Co.: Lobos Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock & Rodriguez* 20852; Tulare Co.: Lake Canyon Creek below Oriole Lake, Sequoia National Park, *Shevock* 17617.

***Pseudobraunia californica* (Lesquereux) Brotherus** [Hedwigiaceae]

Literature: Bourell 1981; Bradshaw 1926; Harthill et al. 1979; Kellman 2003; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Sigal 1975; Steere et al. 1954; Thomson and Ketchledge 1958; Toren 1977; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Braunia californica* Howe 1897; Lesquereux 1868; Lesquereux and James 1884; Watson 1880.

Illustrations: Brotherus 1924–1925; Lawton 1971.
Geographic subdivisions: CaR, CW, GV, NW, SN.
Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris* 87203; Calaveras Co.: Highway 4, 1.2 miles north of Copperopolis, *Shevock* 19327; Glenn Co.: west of town of Elk Creek along Ivory Mill Road, Mendocino National Forest, *Shevock* 15804; Monterey Co.: bluffs at the Pinnacles, Hunter-Leggett Military Reservation, *Norris* 87273; San Benito Co.: Pinnacles National Monument, *J. T. Howell s.n.* (UC); Siskiyou Co.: Soda Creek Road about 4 miles northeast of Interstate 5 near Dunsmuir, Shasta-Trinity National Forest, *Norris* 84799; Tulare Co.: Elk Creek near Potwisha Campground, Middle Fork Kaweah River, Sequoia National Park, *Shevock, Norris, & Barahona* 13186; Yuba Co.: Highway 20 near Timbuc-too, *Norris* 67491.

****Pseudo-calliargon angustifolium* Hedenäs** [Campyliaceae]

Illustrations: Hedenäs 1990.
Geographic subdivisions: SNE.
Selected specimens: Inyo Co.: BLM Warm Springs, Inyo Mountains, *Laeger* 1454 (CAS) [determined by Hedenäs].

****Pseudo-calliargon trifarium* (Weber & D. Mohr) Loeske** [Campyliaceae]

Illustrations: Hedenäs 1990; Smith 1978.
Geographic subdivisions: SN.
Selected specimens: Inyo Co.: east of Pine Creek Pass, John Muir Wilderness, Inyo National Forest, *Weis* 394 (UC) and Gem Lake, Little Lakes Basin, Inyo National Forest, *Weis & Hubbs* 402 (UC).

****Pseudocrossidium crinitum* (Schultz) Zander** [Pottiaceae]

Illustrations: Eckel 1997a; Zander 1993.
Geographic subdivisions: DMoj, DSon, GV, SNE.
Selected specimens: Colusa Co.: Highway 20 at milepost 74, *Norris* 52523 & 52524; Inyo Co.: west

of BLM Goodale Creek Campground, *Norris* 92794 & 92797; San Diego Co.: Palm Canyon, Anza-Borrego State Park, *Norris* 50587; San Bernardino Co.: north slope of Kingston Peak, Kingston BLM Wilderness, *Laeger & Bogan* 1745 (CAS).

***Pseudocrossidium obtusulum* (Lindberg) H. Crum & L. E. Anderson** [Pottiaceae]

Literature: Eckel 1997a; Kellman 2003; Shevock and Toren 2001. As *Pseudocrossidium revolutum* Zander 1981a.

Illustrations: Eckel 1997a; Tan et al. 1981; Zander 1981a.

Geographic subdivisions: CW, DMoj, DSon, NW, SN, SNE, SW.

Selected specimens: Contra Costa Co.: Antioch Dunes National Wildlife Refuge, *Norris* 97036; Kern Co.: near Visitor Center, Red Rock Canyon State Park, *Shevock, Kellman, & Laeger* 20535; Lake Co.: Manning Creek, Highway 175, about 4 miles west of Lakeport, *Toren, Bourell, Dearing, & Shevock* 7002a (CAS); Placer Co.: Highway 49 on north face of American River Canyon, 0.6 mile north of junction of Foresthill Road, *Whittemore* 3518 (CAS, MO); Riverside Co.: South Fork San Jacinto River about 7 miles east of Hemet, *Norris* 58050; San Diego Co.: Box Canyon, Anza-Borrego State Park, *Norris* 50636; San Francisco Co.: Army Street at Highway 101, *Toren* 7820 (CAS); Santa Cruz Co.: Highway 9 about 1.5 miles north of Boulder Creek, *Norris* 55558 & 55560; Trinity Co.: Highway 299 about 3.5 miles northwest of Big Bar, Shasta-Trinity National Forest, *T. Sevelson* 11 (UC).

***Pseudoleskeella serpentinensis* P. Wilson & Norris** [Leskeaceae]

Literature: Wilson and Norris 1989.
Illustrations: Wilson and Norris 1989.

Geographic subdivisions: NW.
Selected specimens: Del Norte Co.: Smith River at Highway 199, Jedediah Smith Redwoods State Park, *Norris* 68927 and Middle Fork Gasquet Road along trail to Stony Creek, *Wilson* 943 & 945 (UC) and west side Smith River about one mile west of Gasquet, *Norris* 70340; Humboldt Co.: junction of Red Mountain and South Red Mountain Road, *Norris* 56452 & 56456; Siskiyou Co.: trail from Wilderness Falls toward Doe Flat, Klamath National Forest, *Norris* 67821 and Doe Creek, *Norris* 23069; Sonoma Co.: The Cedars about 7 miles north of Cazadero, *Robertson* 1580 (CAS) & 1561 (UC).

***Pseudoleskeella tectorum* (Funck ex Bridel) Kindberg ex Brotherus** [Leskeaceae]

Literature: Spjut 1971; Wilson and Norris 1989.
Illustrations: Ignatov and Suragina 2000; Lawton 1971; Lewinsky 1974; Wilson and Norris 1989. As *Leskeella tectorum* Flowers 1973.

Geographic subdivisions: DMoj, SW.
Selected specimens: Inyo Co.: slopes of Rogers

Peak, Panamint Mountains, Death Valley National Park, *Shevock, York, & Davis 21363*; Riverside Co.: summit of Toro Peak, Santa Rosa Mountains, *Harpel 2352* (pers. herb.) and Garnet Queen Creek, Santa Rosa Mountains, San Bernardino National Forest, *Shevock 20528*; San Bernardino Co.: Curtis Canyon, Clark Mountains Wilderness, Mojave National Preserve, *Shevock, Spence, Glazer, & Laeger 23636* and Kingston Peak, Kingston BLM Wilderness, *Laeger & Bogan 1753, 1755, & 1761*.

****Pseudoscleropodium purum* (Hedwig) Fleischer in Brotherus** [Brachytheciaceae]

Illustrations: Buck 1998; Crum and Anderson 1981; Lawton 1971; Smith 1978.

Notes: This species is a recent introduction to the California bryoflora occurring as a coastal lawn weed.

Geographic subdivisions: NW.

Selected specimens: Humboldt Co.: lawns on the campus of Humboldt State University, Arcata, *Norris 71990b*.

***Pseudotaxiphyllum elegans* (Bridel) Iwatsuki** [Hypnaceae]

Literature: Kellman 2003; Shevock and Toren 2001. As *Isopterygium borrierianum* Holmberg 1969; Jamieson 1969. As *Isopterygium elegans* Koch 1950a; Lawton 1971; McGrew 1976; Showers 1982; Yurky 1990, 1995.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Del Norte Co.: Coastal Trail between Requa and False Klamath Cove, Redwood National Park, *Norris 24059*; Humboldt Co.: Prairie Creek Redwoods State Park, *MacFadden 22251* (MO); Mendocino Co.: Simpson Road, Jackson State Forest, *Showers 3193* (SFSU, UC); San Francisco Co.: Mt. Davidson, *Toren 7804* (CAS) and Mt. Sutro, *Shevock 19179*; Shasta Co.: Upper Kings Creek, Lassen Volcanic National Park, *Showers 2257* (SFSU); Siskiyou Co.: near Sugar Lake, Klamath National Forest, *Norris & McGrew 45615*; Sonoma Co.: Gualala River near Lee Noble Road, *Norris 86973*; Trinity Co.: about 1 mile below Rush Creek Lakes, Shasta-Trinity National Forest, *Norris 85406*; Tuolumne Co.: border of Emigrant Wilderness along Burst Rock Trail about 8 air miles east of Strawberry, Stanislaus National Forest, *Norris 82975*.

***Pterigynandrum filiforme* Hedwig** [Pterigynandraceae]

Literature: Howe 1896; Koch 1950a, 1951e; Lawton 1971; Lesquereux 1868; McGrew 1976; Showers 1982; Spjut 1971; Sullivant 1856; Toren 1977; Watson 1880.

Illustrations: Brotherus 1924–1925; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Colusa Co.: about 1.2 miles east of Sites, *Norris 72675*; Fresno Co.: Cedar

Grove along trail between Avalanche and Bubbs Creek, Kings Canyon National Park, *Shevock 13768*; Humboldt Co.: Friday Ridge Road at junction with Titlow Hill Road, Six Rivers National Forest, *Norris 76790*; Lake Co.: Mill Creek, Mt. Sanhedrin, Mendocino National Forest, *Toren 7142* (CAS); Tehama Co.: Battle Creek along Forest Road 29N35 about 4 miles east of Mineral, Lassen National Forest, *Norris 48157*; Trinity Co.: Canyon Creek between Ripstein Camp and McKay Camp, Klamath National Forest, *Norris 7989*; Tulare Co.: Belnap Redwood Grove near Camp Nelson, Sequoia National Forest, *Shevock, Norris, & Barahona 13214*.

***Pterogonium gracile* (Hedwig) J. E. Smith** [Leucodontaceae]

Literature: Bourell 1981; Bradshaw 1926; Brandege 1891; Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Kellman 2003; Kingman 1912; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; McCleary 1972; Mishler 1978; Moxley 1928; Shevock and Toren 2001; Steere 1954; Sullivant 1856; Thomson and Ketchledge 1958; Toren 1977; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Pterogonium gracile* var. *californicum* Cardot and Thériot 1900. As *Pterogonium gracile* var. *duplicato-seratum* Lesquereux 1868; Watson 1880.

Illustrations: Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: CaR, CW, NW, SN, SW.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris 87204*; Fresno Co.: Cedarbrook Picnic area about 1 mile from Highway 245 near Pinehurst, Sequoia National Forest, *Shevock 12815*; Monterey Co.: Big Sur Creek near Pico Blanco Boy Scout Camp, Los Padres National Forest, *Norris 75839*; Riverside Co.: near Lower San Juan Picnic Area, *Norris 58163*; Santa Barbara Co.: Soledad Peak, Santa Rosa Island, Channel Islands National Park, *Shevock & Norris 20747*; Shasta Co.: Fall Creek Road about 1 mile southeast of McCloud Bridge at Shasta Lake, Shasta-Trinity National Forest, *Norris 84861*.

***Pterygoneurum californicum* H. Crum** [Pottiaceae]

Literature: Crum 1967a.

Illustrations: Crum 1967a.

Notes: This species, known only from the type collection, was obtained from an area that is now converted to a mix of urban and agriculture. We have not been able to recollect this species, however, suitable habitat in several nearby preserved landscapes may yet yield a new occurrence.

Geographic subdivisions: GV.

Selected specimens: Kern Co.: alkali flats along Panama Lane, 5 miles west of Highway 99 near Bakersfield, *Koch 4026* (MICH).

****Pterygoneurum lamellatum* (Lindberg) Juratzka** [Pottiaceae]

Illustrations: Flowers 1973; Ignatov and Ignatova 2003; Smith 1978; Zander 1993.
Geographic subdivisions: MP.
Selected specimens: Modoc Co.: salt flats about 9 miles east of Cedarville, *Norris* 47435.

***Pterygoneurum ovatum* (Hedwig) Dixon** [Pottiaceae]

Literature: Crum and Anderson 1981; Koch 1955; Lawton 1971.
Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971; Sharp et al. 1994; Smith 1978; Zander 1993.
Geographic subdivisions: DMOj, DSON, GV, MP, SNE.
Selected specimens: Imperial Co.: Clark Lane south of Coyote Wells, Colorado Desert, *Norris* & *Piippo* 82073; Inyo Co.: Forest Road 7S01, 0.4 mile from Highway 168, Inyo National Forest, *Shevock* 15251 and Wildrose Canyon Road, 1 mile west of Charcoal Kilns, Panamint Mountains, Death Valley National Park, *Shevock* & *Harpel* 19056; Kern Co.: Rosamond Dry Lake, *MacFadden* 3522 (MO) [determined by Delgadillo]; Modoc Co.: about 9 miles east of Cedarville, *Norris* 47447 & 47464 and about 2 miles east of Middle Lake, *Norris* 70421; Tulare Co.: Pixley Vernal Pool Preserve, San Joaquin Valley, *McClintock s.n.* (CAS); Ventura Co.: Quatal Canyon at boundary of Los Padres National Forest, *Norris* 55389 & 80842.

***Pterygoneurum subsessile* (Bridel) Juratzka** [Pottiaceae]

Literature: Koch 1955. As *Pottia subsessilis* Lesquereux 1868; Sullivant 1856.
Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971; Sharp et al. 1994; Zander 1993.
Geographic subdivisions: DMOj, MP.
Selected specimens: Inyo Co.: north of the Race-track, Death Valley National Park, *Norris* 10209h (determined by Crum); Modoc Co.: about 9 miles east of Cedarville, *Norris* 47440, 47455, & 47463.

***Ptychomitrium gardneri* Lesquereux** [Ptychomitriaceae]

Literature: Howe 1896; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Reese 1998; Sigal 1975; Toren 1977; Watson 1880; Yurky 1990, 1995.
Illustrations: Cao and Vitt 1994; Lawton 1971.
Geographic subdivisions: CaR, CW, NW, SN.
Selected specimens: Butte Co.: Big Chico Creek at northeast boundary of Bidwell Park, *Norris* 70045; Contra Costa Co.: Mitchell Canyon, Mt. Diablo State Park, *Koch* 3300 (UC); Humboldt Co.: Quinby Creek about 3 miles north of Denny, *Norris* 52700; Lake Co.: base of Copper Butte, boundary

of Snow Mountain Wilderness, Mendocino National Forest, *Toren & Bourell* 5160 (CAS); Placer Co.: American River, 1 mile east of Rawhide Mines, *MacFadden* 281 (UC); Siskiyou Co.: Highway 3 above junction with Highway 96 overlooking Klamath River, *Shevock* 16888; Tulare Co.: trail to Marble Falls from Potwisha Campground, Marble Fork Kaweah River, Sequoia National Park, *Shevock* 12965.

****Pyramidula tetragona* (Bridel) Bridel** [Funariaceae]

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003.
Geographic subdivisions: CW.
Selected specimens: Santa Barbara Co.: Cherry Canyon above pier, Santa Rosa Island, Channel Islands National Park, *Norris*, *Bratt*, & *Chaney* 102098.

***Racomitrium aciculare* (Hedwig) Bridel** [Grimmiaceae]

Literature: Bourell 1981; Crum and Anderson 1981; Holmberg 1969; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; McGrew 1976; Showers 1982; Spjut 1971; Toren 1977; Watson 1880. As *Grimmia nevii* Howe 1896.
Illustrations: Bednarek-Ochyra 1995; Crum and Anderson 1981; Frye 1917b; Ignatov and Ignatova 2003; Ireland 1982; Koponen et al. 1995; Lawton 1971; Smith 1978; Wagner 1998.
Geographic subdivisions: CaR, CW, NW, SN.
Selected specimens: Fresno Co.: below outlet of Mystery Lake, Dinkey Lakes Wilderness, Sierra National Forest, *Shevock & York* 13922; Humboldt Co.: trail above Bridge Camp west of Clair Eagle Lake, *Norris* 68838; Madera Co.: Forest Highway 81, Chiquito Ridge, Sierra National Forest, *Shevock & Kellman* 19752 (determined by Bednarek-Ochyra); Nevada Co.: near Fuller Lake between Bowman Lake and Highway 20, Tahoe National Forest, *Shevock, Ertter, & Morosco* 15718 (determined by Blom); Santa Cruz Co.: San Lorenzo River below junction with Eagle Creek, *Kellman* 575 (CAS); Tulare Co.: Mineral King, East Fork Kaweah River, Sequoia National Park, *Shevock & O'Brien* 15948 (determined by Blom); Tuolumne Co.: Cherry Creek, Stanislaus National Forest, *Shevock* 19560 (determined by Bednarek-Ochyra).

***Racomitrium affine* (Schleicher ex Weber & D. Mohr) Lindberg** [Grimmiaceae]

Literature: Frisvoll 1988. As *Racomitrium heterostichum* var. *alopecurum* Spjut 1971.
Illustrations: Bednarek-Ochyra 1995; Frisvoll 1988; Fyre 1918a; Smith 1978.
Geographic subdivisions: CaR, NW, SN.
Selected specimens: Lake Co.: east of Cobb Mountain, *Toren & Dearing* 7134 (CAS, KRAM) [determined by Bednarek-Ochyra] and north slope of Kneecap Ridge, tributary of Sheep Creek, Men-

docino National Forest, *Toren* 8835 (CAS) [determined by Bednarek-Ochyra]; Plumas Co.: Butterfly Valley Botanical Area northwest of Quincy, Plumas National Forest, *Laeger* 1589 (CAS, KRAM) [determined by Bednarek-Ochyra].

***Racomitrium depressum* Lesquereux**
[Grimmiaceae]

Literature: Frisvoll 1988; Holmberg 1969; Koch 1950a, 1951e; Lesquereux 1868; Lesquereux and James 1884; Showers 1982; Steere et al. 1954; Watson 1880.

Illustrations: Frisvoll 1988; Frye 1917b.

Geographic subdivisions: CaR, NW, SN, SW.

Selected specimens: Alpine Co.: Pacific Creek at Pacific Valley, Highway 4 east of Pacific Grade Summit, *Norris* 77212; Del Norte Co.: Adams Station along Smith River, *Eastwood* 21461 (MO); Fresno Co.: LeConte Canyon, Kings Canyon National Park, *Shevock & Haultain* 18624 (determined by Bednarek-Ochyra); Madera Co.: Forest Highway 81 near Shakeflat Creek, Sierra National Forest, *Shevock & Kellman* 19746 (determined by Bednarek-Ochyra); Mendocino Co.: Upper Baechtal Canyon near Willits, *Branscomb* 22472 (MO); Nevada Co.: near Fuller Lake, Tahoe National Forest, *Shevock, Ertter, & Morosco* 15718 (determined by Bednarek-Ochyra); Riverside Co.: North Fork San Jacinto River along Seven Pines Trail, San Jacinto State Park, *Harpel* 1097 (CAS, KRAM) [determined by Bednarek-Ochyra]; Tehama Co.: Highway 36 at milepost 96, Lassen National Forest, *Norris* 55978 (determined by Bednarek-Ochyra); Tulare Co.: Twisselmann Botanical Area, south side of Sirretta Pass, Kern Plateau, Sequoia National Forest, *Shevock* 17524 (determined by Blom); Tuolumne Co.: Highway 120 near Tamarack Flat, Yosemite National Park, *Shevock* 18475 (determined by Bednarek-Ochyra).

***Racomitrium elongatum* Ehrhart ex Frisvoll**
[Grimmiaceae]

Literature: Frisvoll 1983; Kellman 2003; Yurky 1995.

Illustrations: Bednarek-Ochyra 1995; Frisvoll 1983; Wagner 1998.

Geographic subdivisions: CW, NW.

Selected specimens: Del Norte Co.: Gasquet-Orleans Road at Kelsey Creek Trail, Six Rivers National Forest, *Norris & Piippo* 82411 and French Hill Road about 3.5 miles above Highway 199 southwest of Gasquet, *Norris* 85054; Lake Co.: Eight Mile Valley, Cow Mountain BLM Recreation Area, *Toren* 6925 (CAS); Mendocino Co.: BLM Road to Red Mountain east of Ukiah, *Norris* 72610; Santa Cruz Co.: Sempervirens Falls, Big Basin Redwoods State Park, *Kellman* 696 (CAS); Trinity Co.: Highway 299 about 2.6 miles east of Del Loma, *Silver* 875 (UC).

***Racomitrium ericoides* (Hedwig) Bridel**
[Grimmiaceae]

Literature: As *Racomitrium canescens* var. *epilolum* Holmberg 1969. As *Racomitrium canescens* var. *ericoides* Holmberg 1969; Lawton 1971.

Illustrations: Bednarek-Ochyra 1995; Frisvoll 1983; Heinonen 1971; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: Pappas Flat 2 miles west of Gasquet, *Norris* 7810; Humboldt Co.: Highway 33 about 11 miles east of Dinsmore, *Norris* 22045; Mendocino Co.: Highway 1 along South Fork Eel River, *Norris* 8567b; Siskiyou Co.: Butler Flat, *Norris* 10177 and 3.5 miles east of Somes Bar, *Norris* 9985; Sonoma Co.: about 1 mile northeast of Baxman Ranch, 10 miles from Plantation, *Koch* 527 (MO).

****Racomitrium fasciculare* (Hedwig) Bridel**
[Grimmiaceae]

Illustrations: Bednarek-Ochyra 1995; Crum and Anderson 1981; Frye 1918a; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: SN.

Selected specimens: Amador Co.: above junction of West and East Fork of Panther Creek, *Norris & Shevock* 103276.

***Racomitrium heterostichum* (Hedwig) Bridel**
[Grimmiaceae]

Literature: Bourell 1981; Crum and Anderson 1981; Frisvoll 1988; Harpel 1980a; Holmberg 1969; Kellman 2003; Koch 1950a, 1951e, 1958; McGrew 1976; Showers 1982; Spjut 1971; Stark and Whittemore 1992; Toren 1977. As *Grimmia heterosticha* Howe 1896.

Illustrations: Bednarek-Ochyra 1995; Crum and Anderson 1981; Frisvoll 1988; Frye 1918a; Ignatov and Ignatova 2003; Ireland 1976, 1982; Smith 1978; Wagner 1998.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Del Norte Co.: Sanger Lake southeast of O'Brien, (Oregon), Siskiyou National Forest, *Norris* 70840; El Dorado Co.: Sly Park Creek, *Norris* 58617; Lake Co.: Forest Road M-1 at Eel River crossing near Lake Pillsbury, Mendocino National Forest, *Toren* 7441 (CAS); Mariposa Co.: Highway 140 near El Portal, Yosemite National Park, *Shevock* 20452 (determined by Bednarek-Ochyra); Placer Co.: Drum Powerhouse Road, Tahoe National Forest, *Shevock & Norris* 20663 (determined by Bednarek-Ochyra); Santa Cruz Co.: Chalk Mountain, Big Basin Redwoods State Park, *Kellman* 1078 (CAS); Siskiyou Co.: northeast of Cook and Green Pass, Rogue River National Forest, *Shevock & Toren* 20105 (determined by Bednarek-Ochyra); Tulare Co.: Redwood Mountain Redwood Grove, Kings Canyon National Park, *Shevock* 17474.

***Racomitrium lanuginosum* (Hedwig) Bridel**

[Grimmiaceae]

Literature: Crum and Anderson 1981.**Illustrations:** Bednarek-Ochyra 1995; Crum and Anderson 1981; Frye 1918a; Ignatov and Cao 1994; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971.**Geographic subdivisions:** CaR, NW.**Selected specimens:** Del Norte Co.: Stony Creek about 1 mile north of Gasquet, North Fork Smith River, *Norris* 9654, 70743 & *Norris & Piippo* 82452; Humboldt Co.: Highway 33 about 11 miles east of Dinsmore, *Norris* 22018; Siskiyou Co.: Interstate 5 at Henley-Hornbrook Exit, *Toren, Mishler, et al.* 7360a (CAS).****Racomitrium lawtonae* Ireland** [Grimmiaceae]**Illustrations:** Ireland 1970, 1976.**Geographic subdivisions:** CaR.**Selected specimens:** Siskiyou Co.: Klamath River at Ash Creek Bridge, Klamath National Forest, *Norris & Hillyard* 105223.***Racomitrium macounii* Kindberg** [Grimmiaceae]**Literature:** Frisvoll 1988. As *Racomitrium heterostichum* var. *macounii* Spjut 1971.**Illustrations:** Bednarek-Ochyra 1995; Frisvoll 1988; Frye 1918a; Wagner 1998. As *Racomitrium sudeticum* var. *macounii* Lawton 1971.**Geographic subdivisions:** CaR, NW, SN.**Selected specimens:** El Dorado Co.: between Wrights Lake and Grouse Lake, Eldorado National Forest, *Norris* 76741; Humboldt Co.: East Fork about 5 air miles north of Mad River, Six Rivers National Forest, *Norris* 83885; Mendocino Co.: Highway 101 at milepost 63 north of Willits, *Norris* 8461; Siskiyou Co.: Haypress Meadows, Marble Mountain Wilderness, Klamath National Forest, *Norris* 12323; Trinity Co.: Highway 299 about 4 miles west of Weaverville, *Norris* 73531.***Racomitrium microcarpon* (Hedwig) Bridel**

[Grimmiaceae]

Literature: Kellman 2003. As *Racomitrium heterostichum* var. *ramulosum* Koch and Ikenberry 1954.**Illustrations:** Bednarek-Ochyra 1995; Frisvoll 1988; Frye 1918a; Ignatov and Ignatova 2003; Smith 1978.**Geographic subdivisions:** CW, SN.**Selected specimens:** Calaveras Co.: about 1 mile west of Salt Springs Reservoir, Stanislaus National Forest, *Norris & Shevock* 103224; Marin Co.: Mt. Tamalpais north of the Mount Theater Parkway, *Robertson* 328 (UC); Santa Cruz Co.: east side Highway 9 near Boulder Creek, *Kellman* 1158 (CAS).****Racomitrium molle* Cardot** [Grimmiaceae]**Illustrations:** No illustration located for this species.**Geographic subdivisions:** NW.**Selected specimens:** Siskiyou Co.: Klamath National Forest, Big Duck Lake, *Norris* 23340, Paynes Lake, *Norris* 46334 and Granite Lake, *Norris* 52324 (determined by Bednarek-Ochyra).***Racomitrium norrisii* Bednarek-Ochyra & Ochyra** [Grimmiaceae]**Literature:** Bednarek-Ochyra and Ochyra 2000.**Illustrations:** Bednarek-Ochyra and Ochyra 2000.**Geographic subdivisions:** SN.**Selected specimens:** El Dorado Co.: along South Fork American River at Carpenter Creek, Eldorado National Forest, *Norris* 58441, 58448b, 58449 & 58468 and South Fork American River at Bridal Veil Campground, Eldorado National Forest, *Norris* 58364; Fresno Co.: South Fork Kings River near Deer Cove Creek, Sequoia National Forest, *Shevock* 14499; Mariposa Co.: Merced River near El Portal, Yosemite National Park, *Shevock & Norris* 20162 and Merced River, Redbud Picnic Area, Sierra National Forest, *Shevock & Norris* 20160 (determined by Bednarek-Ochyra); Tuolumne Co.: Columbia, South Fork Stanislaus River, *Gifford & Ikenberry* 51 (DUKE) [determined by Bednarek-Ochyra].***Racomitrium obesum* Frisvoll** [Grimmiaceae]**Literature:** Frisvoll 1988.**Illustrations:** Frisvoll 1988.**Geographic subdivisions:** CaR, MP, NW, SN.**Selected specimens:** Del Norte Co.: Gasquet-Orleans Road about 3 miles from Big Flat, Six Rivers National Forest, *Norris* 74161 and Poker Creek, Siskiyou National Forest, *Shevock & Toren* 20140 & 20142 (determined by Bednarek-Ochyra); Humboldt Co.: head of Mill Creek along Forest Road 10N02, Six Rivers National Forest, *Norris* 70564; Modoc Co.: Highway 89 at Bear Creek, *Norris* 77952; Nevada Co.: Washington Road near Washington Creek, *Shevock & Toren* 20721 (determined by Bednarek-Ochyra); Siskiyou Co.: West Branch Campground northwest of Happy Camp, Klamath National Forest, *Norris* 75781; Tulare Co.: Redwood Mountain Grove, Kings Canyon National Park, *Shevock* 17476 (determined by Bednarek-Ochyra).***Racomitrium occidentale* (Renauld & Cardot) Renauld & Cardot** [Grimmiaceae]**Literature:** Yurky 1995. As *Racomitrium heterostichum* var. *occidentale* Lawton 1971; Yurky 1990.**Illustrations:** Frisvoll 1988; Frye 1918a; Lawton 1971; Wagner 1998.**Geographic subdivisions:** CaR, CW, MP, NW.**Selected specimens:** Humboldt Co.: Highway 299 about 3 miles west of Willow Creek, *Norris* 12029; Marin Co.: Ridge Trail near Five Brooks, Point Reyes National Seashore, *Yurky* 608 & 868 (SFSU); Mendocino Co.: Fox Creek, Branscomb Reserve of The Nature Conservancy, *Norris* 47150; Shasta Co.: Highway 299 east of Burney at milepost 83, *Norris* 21510; Siskiyou Co.: Forest Road

41N05, 7.5 miles from junction with Forest Road 13, Shasta-Trinity National Forest, *Norris & Hillyard 106461*; Trinity Co.: Flame Gulch near Forest Glen, *Norris 22054*.

***Racomitrium pacificum* Ireland & Spence**

[Grimmiaceae]

Literature: Christy and Wagner 1996; Frisvoll 1988; Ireland and Spence 1987.

Illustrations: Frisvoll 1988; Ireland and Spence 1987; Wagner 1998.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: North Fork Smith River south of Stony Creek, Six Rivers National Forest, *Norris 9636* (determined by Ireland), Gasquet Toll Road at Twelve Mile Creek, Six Rivers National Forest, *Norris 55885* (determined by Bednarek-Ochyra) and Cedar Creek at junction with Smith River, Six Rivers National Forest, *Norris 9687* (determined by Bednarek-Ochyra); Humboldt Co.: junction of Red Mountain Road and South Red Mountain Road, *Norris 56438*; Siskiyou Co.: trail from Wilderness Falls to Doe Flat, Klamath National Forest, *Norris 67745*.

***Racomitrium sudeticum* (Funck) Bruch & W. P. Schimper** [Grimmiaceae]

Literature: Frisvoll 1988. As *Racomitrium heterostichum* var. *sudeticum* McGrew 1976; Showers 1982.

Illustrations: Bednarek-Ochyra 1995; Frisvoll 1988; Frye 1918a; Ignatov and Cao 1994; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Ochyra 1998a; Wagner 1998.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Del Norte Co.: Packsaddle Creek, *Norris 52736*; Humboldt Co.: Quinby Creek about 3 miles north of Denny, *Norris 52690*; Shasta Co.: Shotgun Creek near North Fork Shotgun Creek, south-southeast of Sims, *Norris & Hillyard 103875*; Siskiyou Co.: Long Gulch Lake southwest of Callahan, *Norris 57516*; Trinity Co.: Long Gulch Lake, Klamath National Forest, *Spjut, Norris, & J. Koponen 6287* (UC); Tulare Co.: Mineral King above second Mosquito Lake, Sequoia National Park, *Shevock & O'Brien 15973* (determined by Muñoz) and above Crystal Lake, Mineral King, *Shevock & O'Brien 16009* (determined by Blom).

***Racomitrium varium* (Mitten) A. Jaeger**

[Grimmiaceae]

Literature: Bourell 1981; Holmberg 1969; Kellman 2003; Koch 1950a; Lawton 1971; Spjut 1971; Toren 1977; Yurky 1990, 1995.

Illustrations: Frye 1918a; Lawton 1971; Wagner 1998.

Geographic subdivisions: CW, NW, SN.

Selected specimens: Fresno Co.: South Fork Dinkey Creek below Virginia Lake, Sierra National Forest, *Shevock & York 17419* (determined by Muñoz); Lake Co.: Crab Tree Hot Springs, Mendocino National Forest, *Toren & Dearing 5241* (CAS);

Mendocino Co.: along Covelo Road about 3.1 miles northeast of Longvale, *Norris 21682* and Highway 101 at Dora Creek, *Shevock 20373* (determined by Bednarek-Ochyra); Nevada Co.: Washington Road near Washington Creek, Tahoe National Forest, *Shevock & Toren 20723* (determined by Bednarek-Ochyra); Placer Co.: Dutch Flat Reservoir at dam crossing, *Shevock & Norris 20698* (determined by Bednarek-Ochyra); Santa Cruz Co.: Bonny Doon Ecological Reserve, *Kellman 737* (CAS).

***Rhizomnium glabrescens* (Kindberg) T.**

Koponen [Mniaceae]

Literature: Kellman 2003; Lawton 1971; McGrew 1976; Spjut 1971. As *Mnium glabrescens* Holmberg 1969; Howe 1897; Jamieson 1969; Koch 1950a, 1951e; Thomson and Ketchledge 1958.

Illustrations: Koponen 1973a; Lawton 1971.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Del Norte Co.: Trees of Mystery to Hidden Beach, *Roskell 10003* (UC); Humboldt Co.: Foothill Trail, Prairie Creek Redwoods State Park, *Norris 46016*; Lake Co.: Alder Creek, Cobb Mountain, *Toren & Dearing 7084* (CAS); Mendocino Co.: Road 409 about 1 mile east of Highway 1 south of Fort Bragg, *Norris 11709*; Placer Co.: Big Tree Grove, Tahoe National Forest, *Koch 3154* (UC); San Mateo Co.: along trail near Little Butano Creek, Butano State Park, *Whittemore 4017* (MO); Siskiyou Co.: Crackers Meadow below Young's Peak, *Norris & Ignatov 74765*; Tulare Co.: trail to Heather Lake via Watchtower Loop near junction with Hump Trail, 2 miles from Wolverton, Sequoia National Park, *Shevock 16459*.

***Rhizomnium magnifolium* (Horikawa) T.**

Koponen [Mniaceae]

Literature: McGrew 1976. As *Mnium punctatum* var. *elatum* Crum and Anderson 1981; Koch and Ikenberry 1954. As *Rhizomnium perssonii* Lawton 1971; Spjut 1971.

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: NW, SN.

Selected specimens: Del Norte Co.: near Doctor Rock, *Norris 50344*; Humboldt Co.: headwaters Bunch Grass Creek about 0.9 miles north of Big Hill Road, *Norris 47800*; Mendocino Co.: along County Road 409 west of Highway 1, Jackson State Forest, *R.W. Smith 102* (UC); Siskiyou Co.: Kelly Lake about 12 air miles northwest of Happy Camp, Klamath National Forest, *Norris 83284*; Tulare Co.: west side of First Mosquito Lake, Mineral King, Sequoia National Park, *Shevock & O'Brien 15962*.

***Rhizomnium pseudopunctatum* (Bruch & W. P. Schimper) T. Koponen** [Mniaceae]

Literature: McGrew 1976.

Illustrations: Abramov and Volkova 1998; Ignatov and Ignatova 2003; Lawton 1971; Smith 1978. As

Mnium pseudopunctatum Crum and Anderson 1981.

Geographic subdivisions: NW, SN.

Selected specimens: Fresno Co.: trail from Dutch Lake to Florence Lake, Sierra National Forest, *Norris* 71630; Siskiyou Co.: near Duck Lake, *Norris* 22886 and Sugar Lake, Klamath National Forest, *McGrew* 66, 141, & 199 (UC); Tulare Co.: trail to Heather Lake via the Hump Loop Route, Sequoia National Park, *Shevock* 16503.

***Rhizomnium punctatum* (Hedwig) T. Koponen**
[Mniaceae]

Literature: As *Mnium punctatum* Flowers 1973; Koch 1950a, 1958; Lesquereux 1868; Showers 1982; Watson 1880.

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Smith 1978.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: El Dorado Co.: near Sayles Canyon Trailhead, Eldorado National Forest, *Norris* 70997; Humboldt Co.: north of Orick, Fern Canyon Road west of Highway 101, *Mueller* 6713 (UC); Mendocino Co.: about 4 miles east of Mendocino on Little Lake Road, *Mueller* 6627 (UC); Mono Co.: Lee Vining Grade, Highway 120 about 0.5 mile above Highway 395, *Koch* 1768 (UC).

***Rhytidiadelphus loreus* (Hedwig) Warnstorf**
[Hylocomiaceae]

Literature: Homberg 1969; Ireland 1982; Jamieson 1969; Koch 1950a.

Illustrations: Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CW, NW.

Selected specimens: Humboldt Co.: Prairie Creek Redwoods State Park at James Irvine Trail, *Jamieson* 185 (UC) and 5 miles north of Park Headquarters, *Norris* 68370, Eureka, Jacoby Creek Road at old railroad bridge, *Becking* 65-07-80 (UC), and Greenwood Heights Road about 3.5 miles southeast of Old Arcata Road and 4 miles north of Kneeland, *Norris* 45838 (confirmed by Rohrer); Mendocino Co.: 3 miles south of Piercy, *Flowers* 3966 (NY); San Mateo Co.: Butano Ridge Fire Trail, Butano State Park, *Becking* s.n. (UC); Santa Barbara Co.: cultivated in redwood section of Santa Barbara Botanic Garden, *Laeger* 718 (CAS).

***Rhytidiadelphus squarrosus* (Hedwig) Warnstorf**
[Hylocomiaceae]

Literature: Shevock and Toren 2001.

Illustrations: Abramov and Volkova 1998; Lawton 1971; Smith 1978.

Notes: This species is likely to occur in California only as a lawn weed in the coastal areas.

Geographic subdivisions: CW.

Selected specimens: San Francisco Co.: Japanese Tea Garden, Golden Gate Park, *Toren*, *Showers*, & *Smith* 2811 (CAS, SFSU).

***Rhytidiadelphus triquetrus* (Hedwig) Warnstorf**
[Hylocomiaceae]

Literature: Holmberg 1969; Ireland 1982; Koch 1950a, 1951e; Lawton 1971. As *Hylocomium triquetrum* var. *californicus* Renauld and Cardot 1890.

Illustrations: Abramov and Volkova 1998; Ignatov et al. 1996; Lawton 1971.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Del Norte Co.: French Hill Road about 3.5 miles above Highway 199 southwest of Gasquet, Six Rivers National Forest, *Norris* 85071 and along Forest Road 4803, Siskiyou National Forest, *Norris* 70879; Humboldt Co.: headwaters of Freshwater Creek about 2 miles southeast of Kneeland, *Norris* 68303; Lake Co.: Forest Road 23N56 north of Low Gap west of Round Mountain just south of Glenn County line, Mendocino National Forest, *Toren* 8805 (CAS); Marin Co.: Rock Spring, Mt. Tamalpais State Park, *Robertson* 2038 (CAS); Placer Co.: Canyon Creek near Dutch Flat, *MacFadden* 9796 (MO); Plumas Co.: 1 mile southwest of Meadow Valley Cemetery and 7 miles west of Quincy, Plumas National Forest, *Dillingham* 928 (CAS); Siskiyou Co.: about 1 mile west of White Mountain near Cook and Green Pass, Klamath National Forest, *Norris* 50190, near West Branch Campground on Happy Camp-O'Brien Road, *Norris* 75772 and Elliott Creek near Seattle Bar, Rogue River National Forest, *Shevock* & *Toren* 20088.

****Rhytidiopsis robusta* (W. J. Hooker) Brotherus**
[Hylocomiaceae]

Illustrations: Lawton 1971.

Notes: A rather remarkable range extension into California from the Pacific Northwest considering that this species has yet to be located in the coast redwood region of either Del Norte, Humboldt or Mendocino counties. While a labeling error would be likely to explain this record, this moss was actually brought to the senior author by the collector before it was processed as an herbarium specimen.

Geographic subdivisions: CW, NW (expected).

Selected specimens: San Mateo Co.: Butano Ridge Fire Trail, Butano State Park, *Becking* s.n. (UC).

***Roellia roellii* (Brotherus ex Röhl) Andrews ex H. Crum** [Mniaceae]

Literature: Crum 1967b; Holmberg 1969; McGrew 1976; Showers 1982; Spjut 1971. As *Roellia lucida* Koch 1950a. As *Bryum sandbergii* Flowers 1973; Lawton 1971.

Illustrations: Flowers 1973; Lawton 1971.

Geographic subdivisions: CaR, MP, NW, SN, SNE.

Selected specimens: Del Norte Co.: near Doctor Rock, *Norris* 50324; Glenn Co.: south of Plasket Meadows between Jenks Place and Chimney Rock, Mendocino National Forest, *Toren* & *Isle* 8813 (CAS); Mariposa Co.: Half Moon Meadow to Ten Lakes, Yosemite National Park, *Shevock*, *Wilken*, & *Fritzke* 18486; Modoc Co.: Joseph Creek, Warner

Mountains, Modoc National Forest, *Sanger s.n.* (UC); Mono Co.: Barney Lake, Toiyabe National Forest, *Norris 67128* and Lundy Creek, Hoover Wilderness, *Norris & Hillyard 104123*; Tehama Co.: Middle Fork Beegum Creek about 1.5 miles west of Rat Trap Gap, *Norris 57018*; Tulare Co.: Sawtooth Peak Trail, Mineral King, Sequoia National Park, *Shevock & O'Brien 16036*.

***Sanionia uncinata* (Hedwig) Loeske**

[Campyliaceae]

Literature: As *Drepanocladus uncinatus* Flowers 1973; Ireland 1982; Janssens 1983; Koch 1950a, 1951e, 1958; Lawton 1971; McGrew 1976; Showers 1982; Spjut 1971; Strid 1974. As *Hypnum uncinatum* Lesquereux 1868; Watson 1880.

Illustrations: Flowers 1973; Hedenäs 1989c, 1993a, 2003; Ireland 1982; Janssens 1983; Kanda 1974; Lawton 1971; Ochrya 1998a; Sharp et al. 1998; Smith 1978.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Alpine Co.: Highway 89 at Hope Valley, Toiyabe National Forest, *Norris 48475*; Del Norte Co.: exit of Sanger Lake along Forest Road 4803 southeast of O'Brien (Oregon), Six Rivers National Forest, *Norris 70766*; Inyo Co.: above George Lake west of Bishop, John Muir Wilderness, Inyo National Forest, *Norris 71489* and Inyo Co.: near Golden Trout Lake northwest of Onion Valley, John Muir Wilderness, Inyo National Forest, *Norris 46694*; Siskiyou Co.: Haypress Meadows, Marble Mountain Wilderness, Klamath National Forest, *Norris 12334*; Tulare Co.: Forest Road 14S11 just east of bridge crossing of Big Meadows Creek, Sequoia National Forest, *Shevock & York 13679*.

***Schistidium agassizii* Sullivant & Lesquereux in Sullivant** [Grimmiaceae]

Literature: As *Grimmia agassizii* Crum and Anderson 1981; Flowers 1973; Koch 1950a, 1958; McGrew 1976; Spjut 1971; Strid 1974. As *Grimmia alpicola* Bourell 1981; Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Lawton 1971; McGrew 1976; Showers 1982; Toren 1977.

Illustrations: Blom 1998; Bremer 1980a; Crum and Anderson 1981; Flowers 1973; Holmes 1976; Ignatov and Cao 1994; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971.

Geographic subdivisions: CaR, NW, SN, SNE, SW.

Selected specimens: Inyo Co.: slopes east of Dragon Peak and north of Golden Trout Lake near Onion Valley, John Muir Wilderness, Inyo National Forest, *Norris 46726*; Madera Co.: Jackass Creek above Minarets Road, Sierra National Forest, *Shevock & Kellman 19700* (determined by Blom); Mariposa Co.: below Glacier Point Road along Bridalveil Creek, Yosemite National Park, *Shevock & Norris 20189* (determined by Blom); Siskiyou Co.: Klamath River at Clear Creek, *Norris 10506*; Trinity Co.: Highway 36 at North Fork Rattlesnake

Creek about 4 miles east of Forest Glen, *Norris 23783*; Tulare Co.: Mineral King, East Fork Kaweah River, Sequoia National Park, *Shevock & O'Brien 15947* (determined by Blom); Tuolumne Co.: South Fork Tuolumne River at Highway 120, Yosemite National Park, *Shevock 18473* (determined by Blom); Ventura Co.: Chorro Grande Canyon about 1 mile north of Highway 33, Los Padres National Forest, *Norris 55542*.

***Schistidium atrichum* (C. Müller Hal. & Kindberg) W. A. Weber** [Grimmiaceae]

Literature: As *Grimmia atricha* Flowers 1973; Koch 1949a, 1950a; Lawton 1971; Showers 1982; Toren 1977.

Illustrations: Flowers 1973; Lawton 1971.

Geographic subdivisions: CaR, SW.

Selected specimens: San Bernardino Co.: northeast slope of Mt. San Antonio, Lytle Creek Canyon, San Gabriel Mountains, Angeles National Forest, *Wheeler s.n.* (UC) [determined by Blom]; Siskiyou Co.: Mt. Shasta, Shasta-Trinity National Forest, *Howe s.n.* (NY) [determined by Blom].

***Schistidium cinclidodonteum* (C. Müller Hal. in Röhl) B. Bremer** [Grimmiaceae]

Literature: As *Grimmia cinclidodonteum* Flowers 1973; Harpel 1980a; Harthill et al. 1979; Long 1978; Spjut 1971. As *Grimmia pacifica* Lawton 1979.

Illustrations: Flowers 1973; Lawton 1971; Robinson and Hermann 1964.

Geographic subdivisions: CaR, NW, SN, SNE, SW.

Selected specimens: Alpine Co.: Highway 4 about 4.8 miles west of Ebbetts Pass, Stanislaus National Forest, *Shevock 19963* (determined by Blom); Lake Co.: Upper Nye Camp just north of Snow Mountain Wilderness boundary, Mendocino National Forest, *Shevock, Bourell, & Toren 15839* (determined by Blom); Madera Co.: Minarets Road at Rock Creek, Sierra National Forest, *Shevock & Kellman 19762* (determined by Blom); Riverside Co.: Seven Pines Trail, San Bernardino National Forest, *Harpel 1131* (CAS); Tulare Co.: North Fork Kaweah River at junction with Redwood Creek, Kings Canyon National Park, *Shevock 16642* (determined by Blom).

***Schistidium confertum* (Funck) Bruch & W. P. Schimper** [Grimmiaceae]

Literature: Blom 1996. As *Grimmia apocarpa* var. *conferta* Flowers 1973. As *Grimmia conferta* Lesquereux 1868.

Illustrations: Blom 1996, 1998.

Geographic subdivisions: CaR, CW, NW.

Selected specimens: Contra Costa Co.: south shore of Briones Reservoir, *Norris & Hillyard 106534*; Lake Co.: Crockett Camp Trailhead to Snow Mountain Wilderness, Mendocino National Forest, *Toren & Bourell 5140a* (CAS) and below West Peak, *Toren & Dearing 7469* (CAS) [determined by Blom];

Siskiyou Co.: Mt. Shasta, *Howe s.n.* (NY) [determined by Blom].

***Schistidium dupretii* (Thériot) W. A. Weber**
[Grimmiaceae]

Literature: Blom 1996. As *Grimmia alpicola* var. *dupretii* Harthill et al. 1979; Mishler 1978. As *Grimmia dupretii* Holmberg 1969; Spjut 1971.

Illustrations: Blom 1996, 1998; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971.

Geographic subdivisions: CaR, NW.

Selected specimens: Shasta Co.: Shotgun Creek near North Fork Shotgun Creek, south-southeast of Sims, *Norris & Hillyard 103888*; Siskiyou Co.: between Big Flat and Yellow Rose Mine, *Norris 9116* (COLO) [determined by Blom], Edgar Creek about 3.6 miles east of junction with Forest Road 13, Shasta-Trinity National Forest, *Norris & Hillyard 106480*.

***Schistidium flaccidum* (De Notaris) Ochyra**
[Grimmiaceae]

Literature: Blom 1996. As *Grimmia flaccida* Toren 1977.

Illustrations: Blom 1996, 1998; Lawton 1971.

Geographic subdivisions: CaR, NW, SN, SNE, SW.

Selected specimens: Inyo Co.: trail to Tyee Lakes below South Lake, Inyo National Forest, *Shevock 15280* (determined by Blom); Lake Co.: West Peak Summit, Snow Mountain Wilderness, Mendocino National Forest, *Toren & Dearing 7505* (CAS); Mono Co.: June Lake Loop, Highway 158 above Silver Lake, *Shevock 20043* (determined by Blom); Shasta Co.: north side of Warner Valley below Siford Lakes, Lassen Volcanic National Park, *Showers 2396* (UC); Ventura Co.: above Blue Rock Springs, *Norris 55422*.

***Schistidium maritimum* (Turner ex Scott) Bruch & Schimper** [Grimmiaceae]

Literature: As *Grimmia maritima* Crum and Anderson 1981; Koch 1950a; Lawton 1971.

Illustrations: Blom 1998; Bremer 1980a; Crum and Anderson 1981; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: NW.

Selected specimens: Humboldt Co.: College Cove, Trinidad State Beach, *Silver 902* (UC) and *Norris 47755*, Trinidad Head, *Wolski 2319* (UC) and near Albalone Point, Patricks Point State Park, *Norris 23889*; Mendocino Co.: Russian Gulch State Park, *Koch 3764* (UC).

***Schistidium occidentale* (E. Lawton) Churchill in Funk & D. R. Brooks** [Grimmiaceae]

Literature: As *Grimmia occidentalis* Lawton 1967b, 1971; Showers 1982; Toren 1977; Toren and Sigal 1974.

Illustrations: Lawton 1971.

Geographic subdivisions: SN, SNE, SW.

Selected specimens: Alpine Co.: Highway 4 about 2 miles north of Ebbetts Pass, Toiyabe National Forest, *Shevock 19968* (determined by Blom); Fresno Co.: trail between Crown Creek and Blue Canyon, Kings Canyon National Park, *Shevock & York 14147* (determined by Blom); Inyo Co.: Little Cottonwood Creek near Horseshoe Meadows, Golden Trout Wilderness, *Shevock, Lin, & Chen 17747* (determined by Blom); Los Angeles Co.: Dorr Canyon, Angeles Crest Highway, Angeles National Forest, *Shevock 21659* (determined by Ochyra); Tulare Co.: Nathan's Camp near Rock Creek Ranger Station, Sequoia National Park, *Shevock 18514* (determined by Blom); Tuolumne Co.: Deadman Creek adjacent to Highway 108, 3.5 miles west of Sonora Pass, Stanislaus National Forest, *Shevock 18596* (determined by Blom).

****Schistidium platyphyllum* (Mitten) Persson in Persson & Gjaerev** [Grimmiaceae]

Illustrations: Blom 1998.

Geographic subdivisions: SN.

Selected specimens: Fresno Co.: Cedar Grove just west of Zumwalt Meadows along South Fork Kings River, Kings Canyon National Park, *Shevock 17472* (determined by Blom).

***Schistidium rivulare* (Bridel) Podpěra**
[Grimmiaceae]

Literature: As *Grimmia alpicola* var. *rivularis* Crum and Anderson 1981; Flowers 1973; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Spjut 1971.

Illustrations: Blom 1998; Bremer 1980a; Crum and Anderson 1981; Flowers 1973; Ignatov and Cao 1994; Ignatov and Ignatova 2003; Ireland 1982; Koponen et al. 1995; Lawton 1971; Ochyra 1998a; Sharp et al. 1994.

Geographic subdivisions: CaR, NW, SN, SNE.

Selected specimens: Fresno Co.: LeConte Canyon, Middle Fork Kings River, Kings Canyon National Park, *Shevock & Haultain 18647* (determined by Blom); Lake Co.: Eel River west of Copper Butte and Snow Mountain Wilderness, Mendocino National Forest, *Toren & Bowrell 5164a* (CAS); Mono Co.: Leavitt Creek adjacent to Highway 108, 4.5 miles east of Sonora Pass, Toiyabe National Forest, *Shevock 18603* (determined by Blom); Siskiyou Co.: Big Carmen Lake about 6.5 miles east of Calhahan, Klamath National Forest, *Spjut, Norris, & J. Koponen 6282*; Tehama Co.: Mill Creek about 0.5 mile beyond Mill Creek Campground, *Norris 55937*; Tulare Co.: Marble Fork Kaweah River at Little Deer Creek off of Crystal Cave Road, Sequoia National Park, *Shevock 15637* (determined by Blom); Tuolumne Co.: Tioga Road 0.5 mile west of Siesta Lake, Yosemite National Park, *Shevock 19501* (determined by Blom).

***Schistidium tenerum* (J. E. Zetterstedt) Nyholm**
[Grimmiaceae]

Literature: As *Grimmia tenera* McGrew 1976.

Illustrations: Blom 1996, 1998; Bremer 1980b.

Geographic subdivisions: NW, SN.

Selected specimens: Humboldt Co.: junction of Red Mountain and South Red Mountain Road, *Norris* 56441; Siskiyou Co.: near Bear Lake, *Norris* 24207; Tulare Co.: slopes above Ranger Lakes toward Silliman Pass, Kings Canyon National Park, *Norris* 46587.

***Schizymerium shevockii* A. J. Shaw**
[Meliaceae]

Literature: Shaw 2000.

Illustrations: Shaw 2000.

Geographic subdivisions: SN, SW.

Selected specimens: Fresno Co.: Highway 180 near Yucca Point, Sequoia National Forest, *Shevock* 12468, Boyden Cave, Sequoia National Forest, *Shaw* 9884 (DUKE), trail between Boulder Creek and Boyden Cave, Monarch Wilderness, Sequoia National Forest, *Shevock & York* 13643 (determined by Shaw) and 10 km north of the intersection of Forest Road 9 and Trimmer Balch Camp Road south of Haslett Basin, Sierra National Forest, *Shaw* 9905 & 9907 (DUKE); Mariposa Co.: Highway 140 along Merced River at Slate Creek Bridge, 1 mile west of Sierra National Forest boundary on BLM land, *Shevock* 20467 (confirmed by Shaw); Riverside Co.: San Diego State University Santa Margarita River Ecological Reserve between Temecula and Fallbrook, *Shevock* 20506 (determined by Shaw); Tulare Co.: County Road M-99 near Hospital Flat Campground, Kern River Canyon, Sequoia National Forest, *Shevock* 17038 (determined by Shaw).

***Scleropodium californicum* (Lesquereux)**
Kindberg [Brachytheciaceae]

Literature: Harthill et al. 1979; Howe 1896; Kellman 2003; Koch 1950a; McCleary 1972; Mills-paugh and Nuttall 1923; Sayre 1940; Shevock and Toren 2001; Steere 1954; Thomson and Ketchledge 1958; Whitmore and Sommers 1999; Yurky 1990, 1995. As *Brachythecium californicum* Kingman 1912. As *Hypnum californicum* Brandegee 1891; Lesquereux 1868; Watson 1880.

Illustrations: Sharp et al. 1994.

Geographic subdivisions: CW, NW, SN.

Selected specimens: Humboldt Co.: Eel River about 3 miles north of the start of Avenue of the Giants, *Norris* 72153; Lake Co.: base of Mt. Konocti above Clear Lake at Soda Bay, *Toren & Shevock* 8536 (CAS); Marin Co.: trail near Mud Lake, Point Reyes National Seashore, *Norris* 71824; Mariposa Co.: Summit Road about 2 miles north of Fish Camp, Sierra National Forest, *Norris* 85367; Mendocino Co.: Highway 101 at Cummings turn-off, *Norris* 21616; Monterey Co.: Arroyo Seco Creek about 4 miles west of Greenfield, *Norris* 48501; San Francisco Co.: Alcatraz Island, Golden Gate National Recreation Area, *Shevock, Toren, & Thomas* 20214; Santa Cruz Co.: Majors Creek at Highway 1, *Kellman* 1091 (CAS).

***Scleropodium cespitosum* (Wilson ex C. Müller Hal.) L. Koch** [Brachytheciaceae]

Literature: Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; McCleary 1972; Mishler 1978; Shevock and Toren 2001; Spjut 1971; Thomson and Ketchledge 1958; Toren 1977; Yurky 1990, 1995. As *Hypnum caespitosum* Lesquereux 1868; Watson 1880. As *Scleropodium apocladum* Kingman 1912; Koch 1950a; Koch and Ikenberry 1954; McCleary 1972. As *Scleropodium caespitosum* Bradshaw 1926; Steere 1954.

Illustrations: Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, CW, GV, NW, SN.

Selected specimens: Butte Co.: Big Chico Creek about 3 miles southwest of upper boundary of Bidwell Park, *Norris* 70076; Kern Co.: Highway 178 at Democrat Hot Springs, Kern River Canyon, Sequoia National Forest, *Norris & Piippo* 82208; Mendocino Co.: Greenwood Ridge Road at Navarro River near entrance to Hendy Woods State Park, *Norris* 53106; San Luis Obispo Co.: Lynch Canyon Road about 3 miles from Interlake Road south of San Antonio Reservoir, *Norris* 85156; Santa Cruz Co.: Harvey West Park, City of Santa Cruz, *Kellman* 1238 (CAS); Sonoma Co.: Austin Creek near intersection with Russian River, *Norris* 53139; Stanislaus Co.: sandstone cliff about 2 miles east of Oakdale, *Koch* 1471 (UC).

***Scleropodium colpophyllum* (Sullivant) Grout**
[Brachytheciaceae]

Literature: Kellman 2003; Koch 1950a; Moxley 1928; Shevock and Toren 2001; Steere 1954. As *Eurhynchium colpophyllum* Bradshaw 1926; Howe 1897. As *Hypnum colpophyllum* Watson 1880. As *Scleropodium touretii* var. *colpophyllum* Holmberg 1969; Jamieson 1969; Lawton 1971; Long 1978; Spjut 1971; Toren 1977; Yurky 1990, 1995.

Illustrations: Lawton 1971.

Geographic subdivisions: CW, NW, SN, CW.

Selected specimens: Fresno Co.: Mist Falls Trail near Bubbs Creek junction, South Fork Kings River, Kings Canyon National Park, *Shevock & York* 14467; Humboldt Co.: about 1 mile east of Albee Creek Campground, Humboldt Redwoods State Park, *Norris* 56271; Placer Co.: Drum Forebay Road about 1 mile north of Interstate 80, *Norris* 81988; Riverside Co.: North Fork San Jacinto River near Seven Pines Trail, San Jacinto State Park, *Harpel* 1111 (pers. herb.); Santa Cruz Co.: Highway 8 near San Lorenzo Park north of Boulder Creek, *Norris & Piippo* 82260; Trinity Co.: Corral Bottom Road about 1.5 miles from Big Bar, *Norris* 21038.

***Scleropodium julaceum* E. Lawton**
[Brachytheciaceae]

Literature: Harthill et al. 1979; Kellman 2003; Lawton 1967; Long 1978; Shevock and Toren 2001; Thomson and Ketchledge 1958; Toren 1977; Yurky 1990.

Illustrations: Lawton 1967a.

Geographic subdivisions: CW, SW.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris* 87193; Lake Co.: north shore of Lake Pillsbury at Pogie Point, Mendocino National Forest, *Toren & Bourell* 5045 (CAS); Los Angeles Co.: Sepulveda Canyon, *MacFadden* 18595 (LAM); Monterey Co.: Arroyo Seco Creek about 4 miles west of Greenfield, *Norris* 48505; San Benito Co.: Caves Trail, Pinnacles National Monument, *R. Gantt s.n.* (UC); San Luis Obispo Co.: Highway 166 at Clear Creek, Los Padres National Forest, *Norris* 80666; Santa Cruz Co.: Quail Hollow Ranch County Park, *Kellman* 201 (CAS).

***Scleropodium obtusifolium* (Mitten) Kindberg in Macoun** [Brachytheciaceae]

Literature: Bradshaw 1926; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Howe 1896; Jamieson 1969; Kellman 2003; Kingman 1912; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Long 1978; Mishler 1978; Shevock and Toren 2001; Showers 1982; Spjut 1971; Toren 1977; Yurky 1995.

Illustrations: Flowers 1973; Lawton 1971.

Geographic subdivisions: CaR, CW, MP, NW, SN, SNE, SW.

Selected specimens: Fresno Co.: Grizzly Falls along Highway 180, South Fork Kings River, Sequoia National Forest, *Shevock* 12433; Lake Co.: Upper Nye Camp just north of Snow Mountain Wilderness, Mendocino National Forest, *Shevock, Bourell, & Toren* 15833; Modoc Co.: Crowder Flat Road about 2 miles south of Oregon border, *Norris* 79145; Santa Barbara Co.: about 1 mile south of Bates Canyon Campground, *Norris* 55376; Riverside Co.: Gardner Valley, San Bernardino National Forest, *Harpel* 1954 (pers. herb.) [confirmed by Schofield]; Shasta Co.: Fall Creek Road at Dekkas Rock above Shasta Lake, Shasta-Trinity National Forest, *Norris* 84833.

***Scleropodium touretii* (Bridel) L. Koch** [Brachytheciaceae]

Literature: Bourell 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Kellman 2003; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Long 1978; McCleary 1972; Mishler 1978; Shevock and Toren 2001; Sigal 1975; Smith 1970; Spjut 1971; Toren 1977; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Hypnum illecebrum* Brandege 1891; Lesquereux 1868; Watson 1880. As *Scleropodium illecebrum* Kingman 1912; Millspaugh and Nuttall 1923; Sayre 1940; Steere 1954.

Illustrations: Flowers 1973; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CW, NW, SN, SW.

Selected specimens: Glenn Co.: Highway 36 at Georgie Dells Road, *Norris* 56061; Humboldt Co.: South Fork Mountain Road about 8 air miles north

of Mad River, Six River National Forest, *Norris* 83883; Riverside Co.: near Ortega Oaks Campground, *Norris* 58148; San Mateo Co.: Spring Creek above reservoir, Filoli Center just north of Woodside, *Whittemore & Noyes* 4386 (UC); Tulare Co.: Marble Falls trail above Potwisha Campground, Marble Fork Kaweah River, Sequoia National Park, *Shevock* 12963.

***Scopelophila cataractae* (Mitten) Brotherus** [Pottiaceae]

Literature: Shaw and Anderson 1988; Steen 1986; Zander 1967.

Illustrations: Allen 2002; Crum and Anderson 1981; Sharp et al. 1994; Zander 1967, 1993.

Geographic subdivisions: SN.

Selected specimens: Calaveras Co.: Old Discovery Mine at Copperopolis, *Steen* 810605-2 (CINC, DUKE, UC).

***Scouleria aquatica* W. J. Hooker in Drummond** [Scouleriaceae]

Literature: Bourell 1981; Churchill 1985; Flowers 1973; Holmberg 1969; Howe 1897; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Showers 1982; Spjut 1971; Yurky 1990, 1995. As *Grimmia scouleri* Lesquereux 1868; Lesquereux and James 1884; Watson 1880.

Illustrations: Brotherus 1924–1925; Flowers 1973; Lawton 1971.

Geographic subdivisions: CaR, CW, NW, SN, SNE.

Selected specimens: Amador Co.: below Devil's Lake Trailhead northeast of Bear River Reservoir, Eldorado National Forest, *Norris* 82699; Humboldt Co.: South Fork Tish-Tang-a-Tang Creek east of Hoopa, *Norris & Whittemore* 52390; Inyo Co.: Big Pine Creek adjacent to Glacier Lodge Road, 0.4 miles below Sage Flat Campground, Inyo National Forest, *Shevock* 15323; Lake Co.: tributary of Stony Creek, west slope of Crockett Peak, Snow Mountain Wilderness, Mendocino National Forest, *Toren & Dearing* 7591 (CAS); Marin Co.: Mt. Tamalpais State Park, *J.T. Howell s.n.* (CAS); Mendocino Co.: South Fork Eel River, Branscomb Nature Conservancy Preserve north of Branscomb, *Norris* 47219; Siskiyou Co.: Klamath River at Ishi Pishi Bridge near Somes Bar, Klamath National Forest, *Norris* 12253.

***Scouleria marginata* E. Britton** [Scouleriaceae]

Literature: Christy and Wagner 1996; Churchill 1985; Howe 1896; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Spjut 1971.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Del Norte Co.: Smith River at Highway 199 about 9 miles east of junction with Highway 101, Six Rivers National Forest, *Norris* 85006; El Dorado Co.: South Fork American River at Bridal Veil Falls Campground, Eldorado National Forest, *Norris* 58365; Fresno Co.: South Fork

Kings River at Boulder Creek near Boyden Cave, Sequoia National Forest, *Shevock & York 14508*; Mariposa Co.: Merced River at El Portal, Yosemite National Park, *Norris & Shevock 100241*; Plumas Co.: Highway 89 about 3 miles from Crescent Mills, Plumas National Forest, *Norris 69966*; Siskiyou Co.: Salmon River about 4 miles west of Cecilville, Klamath National Forest, *Norris 10060*; Tulare Co.: North Fork Kern River about 1.5 miles above junction with Little Kern River, Golden Trout Wilderness, Sequoia National Forest, *Shevock 16522*.

***Sematophyllum adnatum* (Michaux) E. Britton**
[Sematophyllaceae]

Literature: Shevock and Toren 2001.

Illustrations: Buck 1998; Sharp et al. 1994.

Geographic subdivisions: CW.

Selected specimens: San Francisco Co.: Mt. Davidson, San Francisco, *Shevock 18929*.

****Sphagnum bartlettianum* Warnstorf**
[Sphagnaceae]

Illustrations: Crum and Anderson 1981.

Geographic subdivisions: NW.

Selected specimens: Mendocino Co.: Pygmy Forest just east of Mendocino. *Andrus 7421* (NY) [determined by Andrus].

***Sphagnum capillifolium* (Ehrhart) Hedwig**
[Sphagnaceae]

Literature: Crum and Anderson 1981; Koch 1950a. As *Sphagnum acutifolium* Lesquereux 1868; Watson 1880.

Illustrations: Crum 1984; Crum and Anderson 1981; Ignatov and Ignatova 2003; Smith 1978.

Geographic subdivisions: NW, SNE.

Selected specimens: Humboldt Co.: Big Lagoon County Park, 13 miles south of Orick, *Silver 899* (UC); Mono Co.: Tioga Junction Campground off of Highway 120, Inyo National Forest, *Norris 48366*.

***Sphagnum compactum* Lamarck & A. P. de Candolle** [Sphagnaceae]

Literature: Crum and Anderson 1981; Warnstorf 1890; Watson 1880. As *Sphagnum rigidum* var. *compactum* Lesquereux 1868.

Illustrations: Crum 1984; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Smith 1978.

Geographic subdivisions: NW, SN.

Selected specimens: Fresno Co.: Marie Lake, *Wheeler 6553* (CAS, DUKE, UC) [determined by Shaw] and above Ranger Lakes near Silliman Pass, Kings Canyon National Park, *Norris 46599* (NY) [determined by Andrus]; Siskiyou Co.: above Big Boulder Lake west of Carrville, Klamath National Forest, *Norris & Streimann 74838*.

****Sphagnum contortum* Schultz** [Sphagnaceae]

Illustrations: Ignatov and Ignatova 2003; Smith 1978.

Geographic subdivisions: NW.

Selected specimens: Mendocino Co.: Pygmy Cypress Forest along Airport Road about 1 mile east of Highway 1 south of Fort Bragg, *Norris 73156*; Siskiyou Co.: Klamath National Forest, near Russian Lake, *McGrew 598* (UC), Lower Russian Lake, *McGrew 304* (UC), Waterdog Lake, *McGrew 470* (UC) [determined by Andrus].

***Sphagnum fimbriatum* Wilson & W. J. Hooker**
[Sphagnaceae]

Literature: Crum and Anderson 1981; Koch 1950a; Lesquereux 1868; Lesquereux and James 1884; Showers 1982; Warnstorf 1890; Watson 1880.

Illustrations: Crum 1984; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Smith 1978.

Geographic subdivisions: NW; SN, SNE.

Selected specimens: Fresno Co.: meadow at base of Maxson Dome, John Muir Wilderness, Sierra National Forest, *Shevock 17442* (determined by Crum) and near Camp 171, eastern base of Mt. Brewer, Kings Canyon National Park, *Brewer 2810* (MO, UC); Humboldt Co.: near McClellan Mountain about 5 miles east of Bridgeville, *Norris 45815, 45816, & 45821* (determined by Andrus); Mono Co.: Cinnabar Canyon north of road to Bodie, *Messick 1539* (UC) [determined by Andrus].

***Sphagnum fuscum* (W. P. Schimper) Klinggräff**
[Sphagnaceae]

Literature: Crum and Anderson 1981; Showers 1982.

Illustrations: Crum 1984; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Smith 1978.

Geographic subdivisions: NW, SN, SNE.

Selected specimens: Fresno Co.: just above first Dinkey Lake, Dinkey Lakes Wilderness, Sierra National Forest, *Shevock & York 13903* (determined by Crum); Glenn Co.: Keller Lake, west slope of Black Butte, Mendocino National Forest, *Toren & Nilles 98-218* (CAS) [determined by Crum]; Mono Co.: Tioga Junction Campground, Highway 120, Inyo National Forest, *Norris 48362* (determined by Andrus); Tulare Co.: Oriole Lake, Sequoia National Park, *Shevock, Norris, & Barahona 13175* (determined by Crum).

****Sphagnum girgensohnii* Russow** [Sphagnaceae]

Illustrations: Crum 1984; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Smith 1978.

Geographic subdivisions: SN, SNE.

Selected specimens: Inyo Co.: near Bishop Lake, John Muir Wilderness, Inyo National Forest, *Shevock & Haultain 18616* (determined by Crum) and Treasure Lake at headwaters of Rock Creek, John Muir Wilderness, Inyo National Forest, *Norris 71555*; Tulare Co.: Moose Lake, Sequoia National

Park, *Munneke, Evens & Roll s.n.* (CAS, DUKE) [determined by Shaw].

Sphagnum henryense Warnstorf [Sphagnaceae]

Literature: Andrus 1980.

Illustrations: Crum 1980, 1984; Crum and Anderson 1981.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: Panther Flats Campground, Highway 199, *Thiers 37513* (SFSU) [determined by Andrus]; Humboldt Co.: near Patrick's Point State Park, *Bourell 1189* (CAS) and Bald Mountain between High Prairie and Snow Camp, *Tracy 4608* (UC) [determined by Andrus]; Mendocino Co.: along Albion-Little River Road south of Mendocino County Airport Landing Strip, *Bourell 3614* (CAS) and 3 miles east of Fort Bragg, *Mason s.n.* (UC) [determined by Andrus].

**Sphagnum inundatum* Russow [Sphagnaceae]

Illustrations: Ignatov and Ignatova 2003; Smith 1978.

Geographic subdivisions: SN.

Selected specimens: Fresno Co.: tributary of Kaiser Creek east of Idaho Lake, Kaiser Wilderness, Sierra National Forest, *Shevock 21002* (determined by Shaw); Madera Co.: Sky Ranch Road, 0.3 mile from Cold Springs Saddle, Sierra National Forest, *Shevock & Kellman 19661* (determined by Shaw); Mariposa Co.: Yosemite Creek below Grant Lakes, Yosemite National Park, *Shevock & Erter 19536* (determined by Shaw); Tulare Co.: meadow east of Sirretta Ridge and Round Meadow, Sequoia National Forest, *Laeger 300 & 301* (CAS, DUKE) [determined by Shaw].

Sphagnum lescurii Sullivant in Gray [Sphagnaceae]

Literature: As *Sphagnum auriculatum* Lesquereux 1868.

Illustrations: No illustration located for this species.

Geographic subdivisions: SN, SNE.

Selected specimens: Fresno Co.: between Wet Meadows and Spanish Lake, John Muir Wilderness, Sierra National Forest, *Shevock 14162*; Inyo Co.: Rock Creek, Inyo National Forest, *Shevock 13812*; Tulare Co.: Deep Meadow about 4 miles north of Quaking Aspen, Sequoia National Forest, *Shevock 17491* (determined by Crum).

Sphagnum magellanicum Bridel [Sphagnaceae]

Literature: Koch 1950a.

Illustrations: Crum 1984; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: SN.

Selected specimens: Fresno Co.: Swamp Meadow below Swamp Lake, Sierra National Forest, *York 2020* (CAS) [determined by Crum]; undetermined county: *James 71* (NY) [determined by Andrus].

Sphagnum mendocinum Sullivant [Sphagnaceae]

Literature: Koch 1950a; Lesquereux and James 1884; Warnstorf 1890; Watson 1880.

Illustrations: Crum 1984.

Geographic subdivisions: NW.

Selected specimens: Humboldt Co.: Patrick's Point, *Tracy 4363* (UC) and shore of Lake Prairie, *Norris 50412*; Mendocino Co.: Albion-Little River Road south of Mendocino County Airport Landing Strip, *Bourell 3616* (CAS), County Road 409, 2.5 miles east of Highway 1, Jackson State Forest, *Smith 84* (UC) and Pygmy Forest along Summers Road east of Fort Bragg, *Norris 23444* and Pygmy Cypress Forest, *Andrus 7416* (MO) [determined by Andrus].

Sphagnum palustre Linnaeus [Sphagnaceae]

Literature: Crum and Anderson 1981; Koch 1950a. As *Sphagnum cymbifolium* Lesquereux 1868.

Illustrations: Crum 1984; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: Panther Flats Campground, Highway 199, *Thiers 37568* (SFSU) [determined by Andrus]; Humboldt Co.: Big Lagoon, *Tracy 6770* (MO, UC) and *Norris 46066*; Mendocino Co.: Albion-Little River Road south of Mendocino County Airport landing airstrip, *Bourell 2077* (CAS) and Pygmy Cypress Forest along Summers Road east of Fort Bragg, *Norris 23441* and Pygmy Cypress Forest, *Andrus 7415* (MO) [determined by Andrus].

**Sphagnum papillosum* Lindberg [Sphagnaceae]

Illustrations: Crum 1984; Ignatov and Ignatova 2003; Ireland 1982; Smith 1978.

Geographic subdivisions: NW.

Selected specimens: Mendocino Co.: about 2.5 miles east of Noyo, *Bacigalupi 6505* (MO, UC), Pygmy Cypress Forest about 5 miles east of Albion, *Norris 11798* and Summers Road east of Fort Bragg, *Norris 23460*, near Fort Bragg, Mitchell Creek, *Thiers 39464* (SFSU) (determined by Andrus) and Pygmy Cypress Forest Preserve, Jackson State Forest, *Showers 3260* (SFSU) [determined by Andrus; Crum].

**Sphagnum platyphyllum* (Lindberg) Warnstorf [Sphagnaceae]

Illustrations: Ignatov and Ignatova 2003; Ireland 1982; Smith 1978.

Geographic subdivisions: NW.

Selected specimens: Mendocino Co.: CA occurrence not specified, *Bolander s.n.* (UC) [determined by Andrus]; undetermined county: *James 70* (NY) [determined by Andrus].

****Sphagnum quinquefarium* (Lindberg in Braithwaite) Warnstorf** [Sphagnaceae]

Illustrations: Crum 1984; Crum and Snider 1977; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Smith 1978.

Geographic subdivisions: NW.

Selected specimens: Mendocino Co.: Pygmy Cypress Forest, 0.5 mile south of Casper east of Highway 1, *Tavares & Sharsmith 729 & 731* (UC), County Road 409, about 1 mile east of Highway 1 south of Fort Bragg, *Norris 11755* (determined by Andrus).

****Sphagnum russowii* Warnstorf** [Sphagnaceae]

Illustrations: Crum 1984; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Smith 1978.

Geographic subdivisions: NW, SN, SNE.

Selected specimens: Fresno Co.: headwaters of Blue Canyon Creek, Kings Canyon National Park, *York 1478* (CAS) [determined by Crum]; Mendocino Co.: Pygmy Cypress Forest along Summers Road east of Fort Bragg, *Norris 23461* (determined by Andrus); Mono Co.: one mile east of Tioga Pass, Inyo National Forest, *J.T. Howell s.n.* (CAS) and *Norris 48364* (determined by Andrus); Tuolumne Co.: Cathedral Lake, Yosemite National Park, *Sharsmith 2196* (UC) [determined by Andrus].

***Sphagnum squarrosum* Crome in Hoppe** [Sphagnaceae]

Literature: Flowers 1973; Crum and Anderson 1981; Koch 1950a; Lesquereux 1868; Lesquereux and James 1884; Showers 1982; Warnstorf 1890.

Illustrations: Crum 1984; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: NW, SN, SNE.

Selected specimens: El Dorado Co.: Grass Lake along Highway 89 west of Luther Pass, Eldorado National Forest, *Norris 71320*; Humboldt Co.: Mill Creek off of Azalea Avenue, McKinleyville, *DeMartini s.n.* (UC) [determined by Andrus]; Mariposa Co.: in spray of Vernal Falls, Merced River, Yosemite National Park, *Eastwood 339* (CAS, MO) [determined by Andrus]; Mono Co.: Junction Campground at road junction to Saddlebag Lake, Inyo National Forest, *Shevock 13781 & 13783* (determined by Crum); Siskiyou Co.: Mud Spring, Middle Creek, *Wheeler 3042* (CAS, DUKE, UC) [determined by Shaw]; Tulare Co.: Ranger Lakes below Silliman Pass, Kings Canyon National Park, *Norris 46599*; Tuolumne Co.: Mt. Dana, Yosemite National Park, *Bolander s.n.* (UC) [determined by Andrus].

***Sphagnum strictum* Sullivant** [Sphagnaceae]

Literature: Crum 1997.

Illustrations: Crum 1984; Crum and Anderson 1981; Ireland 1982; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: SN.

Selected specimens: Fresno Co.: outlet of first Dinkey Lake, Dinkey Lakes Wilderness, Sierra National Forest, *Shevock & York 13885* (determined by Crum).

***Sphagnum subnitens* Russow & Warnstorf** [Sphagnaceae]

Literature: Crum and Anderson 1981. As *Sphagnum plumulosum* Koch 1950a.

Illustrations: Crum 1984; Crum and Anderson 1981; Ignatov and Ignatova 2003; Smith 1978.

Geographic subdivisions: NW, SN.

Selected specimens: Fresno Co.: just north of Potter Pass, Kaiser Wilderness, Sierra National Forest, *Shevock 21025* and near Charlotte Lake, Kings Canyon National Park, *Aken & Munnecke s.n.* (CAS, DUKE) [determined by Shaw]; Humboldt Co.: Big Lagoon County Park, *Norris 48315* (determined by Andrus) and Lake Prairie, *Norris 50411*; undetermined county: *Bolander 211* (NY) [determined by Andrus; Warnstorf].

***Sphagnum subsecundum* Nees in Sturm** [Sphagnaceae]

Literature: Crum and Anderson 1981; Koch 1950a; Lesquereux 1868; McGrew 1976; Showers 1982; Watson 1880.

Illustrations: Crum 1984; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Smith 1978.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: El Dorado Co.: Grass Lake near Luther Pass, Eldorado National Forest, *Bourell 674* (CAS) [determined by Andrus]; Humboldt Co.: Snow Camp Lake, *Norris 50380*; Mariposa Co.: Glacier Point Road at Summit Meadow west of Bridalveil Creek, Yosemite National Park, *Shevock & Norris 20184* (determined by Shaw); Siskiyou Co.: Sugar Lake west of Callahan, Klamath National Forest, *Norris 57375*; Tulare Co.: below Heather Lake, Sequoia National Park, *Shevock 16496* (determined by Crum); Tuolumne Co.: Tiltill Valley, Rancheria Mountain Trail above Hetch Hetchy, Yosemite National Park, *Mason 12067* (UC) [determined by Andrus].

***Sphagnum teres* (W. P. Schimper) Ångström in C. J. Hartman** [Sphagnaceae]

Literature: Crum and Anderson 1981; Koch 1949a, 1950a; Showers 1982. As *Sphagnum squarrosum* Lesquereux 1868.

Illustrations: Crum 1984; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Smith 1978.

Geographic subdivisions: CaR, SN.

Selected specimens: El Dorado Co.: Grass Lake south of Lake Tahoe along Highway 89, Eldorado National Forest, *Stebbins 2315* (UC), *Thorne & Tilforth 39307* (MO, UC), *Norris 71310* and *Andrus 3031 & 7429* (MO) [determined by Andrus]; Nevada Co.: Willow Spring, 2.5 miles west of west end Bowman Lake and 1 mile south of road to

Graniteville, Tahoe National Forest, *Thorne, De-Buhr, & Tilforth 42276* (MO); Placer Co.: Osgood Swamp, *Andrus 7434* (MO, NY); Plumas Co.: Willow Lake Botanical Area, Lassen National Forest, *Shevock & Corbin 12229* and *Austin 370* (UC) [determined by Andrus]; Siskiyou Co.: south side of Mt. Shasta, *H. E. Brown 659* (NY) [determined by Andrus].

***Sphagnum warnstorffii* Russow** [Sphagnaceae]

Literature: Andrus 1979.

Illustrations: Crum 1984; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982.

Geographic subdivisions: SN.

Selected specimens: Fresno Co.: near Bench Lake, Kings Canyon National Park, *Raven s.n.* (CAS, MO) [determined by Blomquist].

***Steerecleus serrulatus* (Hedwig) H. Robinson**
[Brachytheciaceae]

Literature: As *Eurhynchium serrulatum* Spjut 1971.

Illustrations: As *Rhynchostegium serrulatum* Buck 1998; Sharp et al. 1994.

Geographic subdivisions: NW, SW.

Selected specimens: Humboldt Co.: Highway 96 at milepost 18.71 about 7 miles north of Hoopa, *Norris 22290*; Lake Co.: Bartlett Springs Road, *Carmiggelt 52* (UC); Los Angeles Co.: Rubio Canyon, above Pasadena, Angeles National Forest, *McClatchie s.n.* (UC); Siskiyou Co.: about 1 mile west of Elk Lick, *Norris 23276* and 4 miles west of Etna on road to Sawyers Bar, *Norris & Hermann 22667*; Trinity Co.: near Brown's Meadow, *Norris 23170*.

***Stegonia hyalinotricha* (Cardot & Thériot)**
Zander [Pottiaceae]

Literature: As *Phascum hyalinotrichum* Cardot and Thériot 1904; Harthill et al. 1979; Koch 1950a; McCleary 1972; Stark and Whitemore 1992; Steere 1954.

Illustrations: Sharp et al. 1994; Zander 1993.

Geographic subdivisions: CW, GV, MP, SN, SNE, SW.

Selected specimens: Inyo Co.: Big Pine Volcanic Field, BLM Crater Mountain Area of Critical Environmental Concern, west of Highway 395, *Shevock & Newberry 16951*; Kern Co.: Highway 65 near Poso Creek, *Shevock & York 16905* and Highway 178, about 1 mile east of first dam, Kern River Canyon, Sequoia National Forest, *Norris 80776*; Lassen Co.: Highway 138, 3 miles north of Susanville, *Norris 52786 & 52791*, hillside above Johnsondale Dump Road southeast of Susanville, *Norris 52831 & 52832*; Riverside Co.: Santa Margarita Ecological Reserve, *Kellman 1394* (CAS) [determined by Stark]; San Diego Co.: 0.25 mile west of San Vicente Reservoir, 3 miles north of Lakeside, *Stark 578* (MO) and adjacent to and west of Henshaw Lake, Cleveland National Forest, *Stark 636a*

(MO); San Luis Obispo Co.: Nacimiento River at Twin Bridges, Camp Roberts Military Reservation, *Norris 100960*; Santa Barbara Co.: Green Mountain, San Miguel Island, Channel Islands National Park, *Wheeler 8031* (CAS, UC).

****Stegonia latifolia* (Schwägrichen in Schultes)**
Venturi ex Brotherus [Pottiaceae]

Illustrations: Ochyra 1998a; Zander 1993. As *Pottia latifolia* Lawton 1971.

Geographic subdivisions: CaR, MP, SN.

Selected specimens: Fresno Co.: near summit of Dogtooth Peak, Dinkey Lakes Wilderness, Sierra National Forest, *York 1217* (CAS); Lassen Co.: Highway 395 about 3 miles north of Litchfield at milepost 79.7, *Norris 22596*; Tehama Co.: Highway 36, 56 miles east of Shasta County line, *Norris 8745*.

***Stegonia pilifera* (Bridel) H. Crum & L. E. Anderson** [Pottiaceae]

Literature: As *Stegonia latifolia* var. *pilifera* Crum 1957.

Illustrations: Flowers 1973. As *Pottia latifolia* var. *pilifera* Lawton 1971.

Geographic subdivisions: MP, SN, SNE.

Selected specimens: Fresno Co.: Mt. Barnard, Sierra National Forest, *Raven s.n.* (CAN, CAS) [determined by Crum]; Lassen Co.: Highway 395 about 3 miles north of Litchfield at milepost 79.7, *Norris 22597*; Modoc Co.: about 9 miles east of Cedarville, *Norris 47445*; Mono Co.: White Mountain Peak, White Mountains, Inyo National Forest, *York 2453* (CAS).

***Straminergon stramineum* (Dickson ex Bridel)**
Hedenäs [Campyliaceae]

Literature: As *Calliergon stramineum* Koch 1949a, 1950a, 1958; Showers 1982.

Illustrations: Flowers 1973; Hedenäs 1993a, 2003; Ireland 1982; Kanda 1978; Lawton 1971; Smith 1978.

Geographic subdivisions: SN, SNE.

Selected specimens: El Dorado Co.: Grass Lake along Highway 89, Eldorado National Forest, *Norris 79044*; Fresno Co.: between Marvin Pass and Mitchell Peak trail junction, Jennie Lakes Wilderness, Sequoia National Forest, *Shevock 14558*; Inyo Co.: Treasure Lake, John Muir Wilderness, Inyo National Forest, *Norris 71563*, Hearst Lake Trail from Onion Valley, *Norris 46784* and Robinson Lake, Inyo National Forest, *Norris 46644*.

***Syntrichia amplexa* (Lesquereux) Zander**
[Pottiaceae]

Literature: Kellman 2003; Shevock and Toren 2001. As *Barbula amplexa* Brandegees 1891; Lawton 1971; Lesquereux 1868; Watson 1880. As *Tortula amplexa* Harthill et al. 1979; Koch 1950a; Koch and Ikenberry 1954; Toren 1977; Yurky 1990, 1995.

Illustrations: Lawton 1971; Smith 1978.

Geographic subdivisions: CW, NW.

Selected specimens: Humboldt Co.: about 1 mile east of Payton Ranch north of Blocksburg, *Norris* 48195; Lake Co.: east of Hell's Peak near Bachelor Valley, *Toren* 1049 (SFSU); Marin Co.: Angel Island State Park, *J.T. Howell s.n.* (CAS); Monterey Co.: Pacific Grove, Monterey, *M. Howe s.n.* (UC); San Francisco Co.: China Beach, Golden Gate National Recreation Area, *Shevock* 19270; Santa Cruz Co.: at beach, Rancho del Oso Division, Big Basin Redwoods State Park, *Kellman* 1214 (CAS); Sonoma Co.: near Petaluma, *Koch* 1319 (UC).

***Syntrichia bartramii* (W. C. Steere in Grout) Zander** [Pottiaceae]

Literature: Kellman 2003. As *Tortula bartramii* Harpel 1980a; Harthill et al. 1979; Koch 1950a; Lawton 1971; Long 1978; McGrew 1976; Mishler 1978.

Illustrations: Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: CW, DMoj, MP, SNE, SW.

Selected specimens: Inyo Co.: Long Lake near Morgan Pass, John Muir Wilderness, Inyo National Forest, *Shevock* 13818 and Rogers Peak near Hummingbird Spring, Death Valley National Park, *York & Davis* 2703 (CAS); Lassen Co.: Highway 395 about 3 miles north of Litchfield at milepost 79.7, *Norris & Hermann* 22598; Riverside Co.: Marion Mountain Campground, San Jacinto Mountains, San Bernardino National Forest, *Harpel* 31 (pers. herb.); San Luis Obispo Co.: Boy Scout Road, Camp Roberts Military Reservation, *Norris* 100903; Santa Cruz Co.: south of Eagle Rock near Bonny Doon, *Kellman* 867 (BUF, CAS) [determined by Zander].

***Syntrichia bolanderi* (Lesquereux & T. P. James) Zander** [Pottiaceae]

Literature: Kellman 2003; Shevock and Toren 2001. As *Barbula bolanderi* Bradshaw 1926; Brandege 1891; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Watson 1880. As *Tortula bolanderi* Harthill et al. 1979; Howe 1896; Koch 1950a, 1951e; Koch and Ikenberry 1954; McCleary 1972; Mishler 1978; Steere 1954; Steere et al. 1954; Toren 1977; Whittemore and Sommers 1999; Yurky 1990, 1995.

Illustrations: Lawton 1971.

Geographic subdivisions: CW, NW, SN, SW.

Selected specimens: Lake Co.: road to Harbin Springs near Boggs Mountain, *Toren & Dearing* 7282 (CAS); San Luis Obispo Co.: Queen Bee Campground about 1 mile east of La Panza Summit, *Norris* 55177; Santa Cruz Co.: Laurel Road at Highway 17, *Kellman* 2650 (CAS); Sonoma Co.: Russian Gulch Creek about 0.25 mile from Highway 1, *Koch* 3505 (UC); Riverside Co.: South Fork San Jacinto River about 7 miles east of Hemet, *Norris* 58056; Tehama Co.: end of Buckhorn Road, Black Butte Recreation Area, *Norris & Piippo* 82391; Tulare Co.: Wishon Road at Dunn Fire

Trail, Sequoia National Forest, *Norris, Shevock, & Barahona* 87034.

***Syntrichia caninervis* Mitten** [Pottiaceae]

Literature: As *Tortula bistratosa* Harpel 1980a; Harthill et al. 1979; Lawton 1971; Long 1978; Toren 1977.

Illustrations: Ignatov and Ignatova 2003; Lawton 1971.

Geographic subdivisions: DMoj, DSon, MP, NW, SNE.

Selected specimens: Inyo Co.: Forest Road 7S01, 0.4 mile from Highway 168 west of Bishop, Inyo National Forest, *Shevock* 15252 and Emigrant Canyon Road at Aguerberry Point Road, Panamint Mountains, Death Valley National Park, *Shevock & Harpel* 19055; Kern Co.: Sand Canyon just off Highway 58, *Shevock* 13236; Lake Co.: Highway 20 east of Highway 53 junction at Grizzly Spring, *Toren* 6821 (CAS) [determined by Mishler]; Lassen Co.: narrow canyon along Amedee Canyon north of Honey Lake, *Norris* 80992; Modoc Co.: about 9 miles east of Cedarville along Highway 299, *Norris* 47460 & 47474; San Bernardino Co.: Granite Mountains, Mojave National Preserve, Mojave Desert, *Norris, Shevock, & Barahona* 87745.

***Syntrichia laevipila* Bridel** [Pottiaceae]

Literature: Kellman 2003. As *Barbula laevipila* Lesquereux 1868; Lesquereux and James 1884; Watson 1880. As *Tortula laevipila* Harpel 1980a; Harthill et al. 1979; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; McCleary 1972; Mishler 1978; Spjut 1971; Steere 1954; Steere et al. 1954; Thomson and Ketchledge 1958; Toren 1977; Whittemore and Sommers 1999.

Illustrations: Lawton 1971; Smith 1978; Zander 1993.

Notes: Dr. Brent Mishler of U.C. Berkeley has pointed out (personal communication) that the California collections labeled as *Syntrichia laevipila* differ in many respects from the type collection of the species (Europe). The California material upon further study may require a different circumscription. This will be addressed in the *Syntrichia* treatment for the Bryophyte Flora North America (BFNA).

Geographic subdivisions: CaR, CW, GV, NW, SN, SW.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris* 87189; Kern Co.: Bloomfield Ranch adjacent to South Fork Kern River, Kern Plateau, *Shevock* 12126a; Los Angeles Co.: West Fork San Gabriel River, San Gabriel Mountains, Angeles National Forest, *Harpel* 2208 (pers. herb.); Mendocino Co.: Highway 101 at Cummings turnoff, *Norris* 21631; Modoc Co.: near Post Canyon north of Adin, *Norris* 47410; San Diego Co.: about 1 mile north of Cuyamaca State Park Headquarters, *Norris* 50716; Shasta Co.: Highway 299 at Crystal Creek, Whiskeytown National Recreation Area, *Norris & Hillyard* 105423;

Sutter Co.: Philip Road near junction with Fiddyment Road northwest of Roseville, *Norris* 103673 & 103796.

****Syntrichia laevipila* Bridel var. *meridionalis* (W.P. Schimper) Juratzka** [Pottiaceae]

Illustrations: Kellman 2003; As *Tortula laevipila* var. *meridionalis* Lawton 1971.

Geographic subdivisions: CW, NW.

Selected specimens: Lake Co.: Middletown City Park on valley oak, *Toren* 7349 (CAS) and east shore Clear Lake at town of Nice, *Toren* 7708 (CAS) [confirmed by Mishler]; Santa Cruz Co.: San Lorenzo Valley, Quail Hollow Ranch County Park, *Kellman* 945 (CAS).

***Syntrichia latifolia* (Bruch ex C. J. Hartman) Hübener** [Pottiaceae]

Literature: Jamieson 1969; Kellman 2003; Koch 1950a, 1951e; Lawton 1971; Shevock and Toren 2001; Toren 1977. As *Barbula latifolia* Lesquereux 1868; Lesquereux and James 1884; Watson 1880.

Illustrations: Lawton 1971; Smith 1978.

Geographic subdivisions: CW, GV, MP, NW, SN.

Selected specimens: Fresno Co.: Big Creek at Blue Canyon near Bretz Campground, Sierra National Forest, *Norris*, *Shevock*, & *Barahona* 87401; Mendocino Co.: East Side Road at Knight Hill along Russian River about 8 miles south of Ukiah, *Norris* 72652; Modoc Co.: Pin Creek Campground east of Likely, *Norris* 9436; San Francisco Co.: Lafayette Park, *Shevock* 19236; Santa Cruz Co.: north of Soda Lake near Chittendon, *Kellman* 921 (CAS); Shasta Co.: about 2.3 miles east of Anderson on road to Olinda, *Norris* 47625; Tehama Co.: Sacramento River at Woodson Bridge State Park, *Norris* 50423; Tulare Co.: Mineral King, slopes above Eagle Lake Creek just below Eagle Lake, Sequoia National Park, *Shevock* & *O'Brien* 15986.

***Syntrichia norvegica* Weber** [Pottiaceae]

Literature: As *Tortula norvegica* Crum and Anderson 1981; Harpel 1980a; Harthill et al. 1979; Koch 1950a, 1951e; Lawton 1971; Long 1978; Showers 1982; Spjut 1971.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Sharp et al. 1994.

Geographic subdivisions: DMoj, NW, SN, SNE, SW.

Selected specimens: Alpine Co.: above Red Lake Creek, Toiyabe National Forest, *Norris* 88128; Humboldt Co.: road to Eight Mile Lookout about 1 mile west of South Fork Mountain Road, Six Rivers National Forest, *Norris* 83873; Kern Co.: Scodie Mountains about 1 mile west of Walker Pass off of Highway 178, *Norris*, *Shevock*, & *Barahona* 87121; Lake Co.: north cirque of Hull Mountain, Mendocino National Forest, *Toren* & *Dearing* 7232 (CAS); San Diego Co.: Mesa Picnic Area, O'Neal Regional Park south of Lower Otay Reservoir, *Norris* & *Piippo* 82173; Tulare Co.: below Paradise

Ridge near Paradise Cave, Sequoia National Park, *Shevock* 14641.

***Syntrichia obtusissima* (C. Müller Hal.) Zander** [Pottiaceae]

Literature: As *Tortula obtusissima* Harthill et al. 1979; Koch 1950a.

Illustrations: Sharp et al. 1994.

Geographic subdivisions: DMoj, DSon, SN, SNE, SW.

Selected specimens: Kern Co.: Highway 178 below Walker Pass about 2 miles northwest of Cranebrake Creek, Scodie Mountains, *Kellman* 1442 (CAS); Riverside Co.: Snakeye Springs, Indian Cove, Joshua Tree National Park, *Norris* 57971 & 57999 and along Highway 74 at eastern boundary of San Bernardino National Forest below Bighorn Overlook, *Norris* 57860.

***Syntrichia pagorum* (Milde) Amann** [Pottiaceae]

Literature: Shevock and Toren 2001. As *Tortula pagorum* Anderson 1943; Crum and Anderson 1981; Harpel 1980a; Kellman 2003; Koch 1949a, 1950a; Yurky 1990, 1995.

Illustrations: Crum and Anderson 1981; Sharp et al. 1994; Stone 1971; Zander 1993.

Geographic subdivisions: CaR, CW, GV, NW, SW.

Selected specimens: Alameda Co.: University of California Berkeley Campus, *Thornburg s.n.* (UC); Butte Co.: City Square of Gridley, *Norris* 52539; Riverside Co.: Soboba Indian Reservation, San Jacinto Mountains, *Harpel* 1348 (pers. herb.); Sacramento Co.: Capitol Park at 15th and L Street, Sacramento, *Shevock* 12582; San Francisco Co.: Panhandle, Golden Gate Park, *Toren* 7799 (CAS) and Alamo Square, *Shevock* 18910; Santa Cruz Co.: Zayante Trail, Henry Cowell Redwoods State Park, *Kellman* 641 (UC); San Luis Obispo Co.: Tower Road near west end of Camp Roberts Military Reservation, *Norris* 100876; Tehama Co.: Black Butte Reservoir, *Norris* 50444.

***Syntrichia papillosa* (Wilson in Spruce) Juratzka** [Pottiaceae]

Literature: Crum and Anderson 1981; Harthill et al. 1979; Kellman 2003; Koch 1950a; Schnooburger 1942; Shevock and Toren 2001.

Illustrations: Crum and Anderson 1981; Ireland 1982; Schnooburger 1942; Sharp et al. 1994; Zander 1993.

Geographic subdivisions: CW, NW, SW.

Selected specimens: Alameda Co.: University of California Berkeley campus, *Shevock* & *Norris* 24478; Lake Co.: Highway 175 at Middletown, *Toren* 7250 (CAS); San Bernardino Co.: Meadowbrook City Park, City of San Bernardino, *Harpel* 785 (pers. herb.); San Francisco Co.: Lafayette Park, *Shevock* 19251; Santa Cruz Co.: near Eagle Rock, *Kellman* 869 (CAS).

****Syntrichia papillosissima* (Coppey) Loeske**

[Pottiaceae]

Illustrations: As *Tortula papillosissima* Flowers 1953, 1973; Lawton 1971; Sharp et al. 1994. As *Tortula ruralis* var. *hirsuta* Harpel 1980a. See also Bizot 1954, 1965.

Geographic subdivisions: CaR, CW, MP, SN, SW.

Selected specimens: Fresno Co.: canyon west of Boyden Cave, Monarch Wilderness, South Fork Kings River, Sequoia National Forest, *Shevock & York 12338*; Lassen Co.: slopes of Shaffer Mountain north of Honey Lake, *Norris 76305*; Mariposa Co.: Yosemite Valley, Yosemite National Park, *Kellman 521* (CAS); Monterey Co.: along Arroyo Seco Creek about 4 miles west of Greenfield, *Norris 48504*; Modoc Co.: along Pepperdine Trail, South Warner Wilderness, Modoc National Forest, *Sanger s.n.* (UC); San Diego Co.: about 1 mile north of Cuyamaca State Park Headquarters, *Norris 50715*; Siskiyou Co.: Shasta River about 2 miles south of junction with Klamath River, *Norris 102954*.

***Syntrichia princeps* (De Notaris) Mitten**

[Pottiaceae]

Literature: Kellman 2003; Shevock and Toren 2001. As *Barbula muelleri* Lesquereux 1868; Sullivant 1856; Watson 1880. As *Tortula princeps* Bourell 1981; Bradshaw 1926; Cooke 1941; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; Long 1978; McCleary 1972; McGrew 1976; Mishler 1978; Showers 1982; Sigal 1975; Spjut 1971; Steere et al. 1954; Strid 1974; Thomson and Ketchledge 1958; Toren 1977; Whittemore and Sommers 1999; Yurky 1990, 1995.

Illustrations: Flowers 1973; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CaR, CW, MP, NW, SN, SW.

Selected specimens: Fresno Co.: Horseshoe Bend along Highway 180, South Fork Kings River, Sequoia National Forest, *Shevock & York 12324*; Lake Co.: Clear Lake State Park, *Norris 47718*; Orange Co.: Upper Trabuco Canyon, Santa Ana Mountains, Cleveland National Forest, *Shevock 3989 & 3993*; Placer Co.: about 1 mile below Drum Powerhouse, *Norris 82001*; San Mateo Co.: Flume Trail near Boulder Creek Bridge just north of Woodside, *Whittemore 4406* (UC).

***Syntrichia ruralis* (Hedwig) Weber & D. Mohr**

[Pottiaceae]

Literature: Shevock and Toren 2001. As *Barbula ruralis* Sullivant 1856. As *Tortula intermedia* Holmberg 1969; Koch 1950a; Koch and Ikenberry 1954; Sayre 1940; Sigal 1975; Spjut 1971; Steere 1954. As *Tortula ruraliformis* Koch 1950a. As *Tortula ruralis* Bourell 1981; Bradshaw 1926; Coville 1893; Crum and Anderson 1981; Harpel 1980a;

Harthill et al. 1979; Jamieson 1969; Kingman 1912; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Lesquereux and James 1884; Long 1978; McCleary 1972; McGrew 1976; Mishler 1978; Showers 1982; Spjut 1971; Strid 1974; Toren 1977; Yurky 1990, 1995. As *Tortula ruralis* var. *crinita* Harpel 1980a; Mishler 1978. As *Tortula montana* Howe 1897; Millspaugh and Nuttall 1923.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978; Zander 1993.

Geographic subdivisions: CaR, CW, DMoj, DSon, MP, NW, SN, SNE, SW.

Selected specimens: Kern Co.: Kelso Creek Road about 2 miles south of Bird Springs Pass junction, *Shevock 14883*; Los Angeles Co.: between Black Jack Campground and Orizaba Mountain, Santa Catalina Island, *Shevock & Thorne 4035*; San Bernardino Co.: Granite Mountains, Mojave National Preserve, *Norris, Shevock, & Barahona 87762*; San Diego Co.: Old Highway Road near Bankhead Springs, *Norris & Piippo 82116*; San Mateo Co.: Lake Pilarcitos, *Koch 3371* (UC); Shasta Co.: Coffee Creek at East Fork Coffee Creek, *Norris & Hermann 22585*.

***Tetraphis pellucida* Hedwig** [Tetraphidaceae]

Literature: Ireland 1982; Jamieson 1969; Koch 1950a; Lawton 1971; Lesquereux 1868; Smith 1970; Spjut 1971; Watson 1880; Weber and Simone 1977.

Illustrations: Abramov and Volkova 1998; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: NW, MP.

Selected specimens: Del Norte Co.: Smith River, Jedediah Smith State Park, *Norris 67354* and along Highway 299 about 2 miles west of campground, *Norris 85075*; Humboldt Co.: Prairie Creek Redwoods State Park, *Jamieson 286* (UC); Mendocino Co.: County Road 409 about 1 mile east of Highway 1 south of Fort Bragg, *Norris 11714*; Modoc Co.: Upper Rush Creek Campground about 8 miles north of Adin on Highway 299, *Norris, Nelson, & Dowty 19448*; Siskiyou Co.: between Tickner Creek and Blue Granite Lake, Klamath National Forest, *Norris 52278*.

***Thamnobryum neckeroides* (W. J. Hooker) E.**

Lawton [Neckeraceae]

Literature: As *Thamnobryum leibergii* Spjut 1971.

Illustrations: Lawton 1971.

Geographic subdivisions: NW.

Selected specimens: Humboldt Co.: Tish-Tang-a-Tang Creek near Grogans Hole, Six Rivers National Forest, *Norris 47727*; Siskiyou Co.: about 1 mile east of Copper Butte, Klamath National Forest, *Norris 50236* and Haypress Meadows, Marble Mountain Wilderness, Klamath National Forest, *Norris 12390*; Tehama Co.: Beegum Basin, north

slope of North Yolla Bolly Mountain, Shasta-Trinity National Forest, *Norris* 57040.

***Timmia austriaca* Hedwig** [Timmiaceae]

Literature: Brassard 1980; Crum and Anderson 1981; Holmberg 1969; Lawton 1971; Miller and Ireland 1978; Showers 1982; Spjut 1971.

Illustrations: Brassard 1979, 1980; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Mastracci 1993; Miller and Ireland 1978; Smith 1978.

Geographic subdivisions: CaR, NW.

Selected specimens: Del Norte Co.: Packsaddle Creek, *Norris* 52727 and South Siskiyou Fork below Prescott Cabin, Six Rivers National Forest, *Norris* 47923; Humboldt Co.: South Fork Tish-Tang-a-Tang Creek east of Hoopa, *Norris* & *Whitemore* 52386; Shasta Co.: Chaos Crags, Lassen Volcanic National Park, *Showers* 3739 (SFSU); Siskiyou Co.: Sugar Creek just east of Eaton Peak, Trinity Alps, Klamath National Forest, *Spjut, Norris*, & *J. Koponen* 6265 (UC), Salmon River near Big Flat, *Norris* 9183 and above Applegate River on road toward Cook and Green Pass, Rogue River National Forest, *Shevock* & *Toren* 20121.

***Timmia bavarica* Hessler** [Timmiaceae]

Literature: As *Timmia megapolitana* var. *bavarica* Crum and Anderson 1981.

Illustrations: Brassard 1979; Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971; Mastracci 1993; Sharp et al. 1994.

Geographic subdivisions: DMoj, SNE.

Selected specimens: Inyo Co.: Methuselah Trail, Schulman Grove, Ancient Bristlecone Pine Forest Botanical Area, White Mountains, Inyo National Forest, *Norris* 46837 & 46852 and Mt. Birch, John Muir Wilderness, Inyo National Forest, *Laeger* 188 (CAS); San Bernardino Co.: summit of Kingston Peak, BLM Kingston Wilderness, Mojave Desert, *Laeger* & *Bogan* 1762 (CAS) [determined by Brassard].

***Timmia anomala* (Bruch in W. P. Schimper) Limpricht** [Pottiaceae]

Literature: Harthill et al. 1979; Koch 1950a; Long 1978; McCleary 1972; Shevock and Toren 2001; Showers 1982. As *Trichostomum anomalum* Brandege 1891; Lesquereux 1868; Lesquereux and James 1884; Watson 1880.

Illustrations: Allen 2002; Crum and Anderson 1981; Sharp et al. 1994; Zander 1993.

Geographic subdivisions: CW, SN, SW.

Selected specimens: El Dorado Co.: Highway 193 at Garden Valley Road, *Norris* & *Piippo* 82308; Fresno Co.: Spanish Mountain Jeep Road, Sierra National Forest, *Shevock* & *York* 12402; Monterey Co.: Salmon Creek Trail, Santa Lucia Range, Los Padres National Forest, *Norris* 68227; Riverside Co.: Ortega Oaks Campground, Cleveland National Forest, *Norris* 58105 & 58130; San Diego Co.: Flinn Springs County Park, *Norris* 50669 and Mir-

amar Road near Miramar Air Station, *Norris* 50694; San Francisco Co.: Bernal Heights Park, *Shevock* 19258.

***Timmia crassinervis* (Hampe) L. Koch** [Pottiaceae]

Literature: Bourell 1981; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Long 1978; Mishler 1978; Shevock and Toren 2001; Smith 1970; Strid 1974; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Timmia flexisetata* Kingman 1912. As *Timmia vancouveriensis* Kingman 1912; Steere 1954; Steere et al. 1954. As *Trichostomum flavo-virens* var. *crassinerve* Lesquereux and James 1884. As *Trichostomum flexipes* Brandege 1891; Lesquereux 1868; Lesquereux and James 1884; Sullivant 1856; Watson 1880.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, CW, NW, SN.

Selected specimens: Butte Co.: Big Chico Creek, Upper Bidwell Park, Chico, *Janeway* 5514 (MO); Del Norte Co.: Smith River about 16 miles east of Gasquet along Highway 199, Six Rivers National Forest, *Norris* 8879; Lake Co.: Highway 53 about 1 mile south of Highway 20, *Norris* 47699; Madera Co.: Highway 41 at intersection of North Fork Road, *Norris* 51036; San Francisco Co.: McLaren Park, *Shevock* 19139; San Luis Obispo Co.: Foxen Canyon Road about 8 miles north of Los Olivos, *Norris* 68178; Santa Cruz Co.: Forest of Nisene Marks State Park, *Kellman* 212 (CAS); Siskiyou Co.: near Bear Lake, *Norris* 24193; Tulare Co.: Belknap Grove near Camp Nelson, Sequoia National Forest, *Norris* 50909.

****Tortella alpicola* Dixon** [Pottiaceae]

Illustrations: As *Tortella tortelloides* Eckel 1991. See Eckel (1997a) for discussion on this species.

Geographic subdivisions: NW.

Selected specimens: Lake Co.: canyon below Forest Road M-3 at Low Gap, Mendocino National Forest, *Shevock, Bourell*, & *Toren* 15866 [determined by Eckel] and *Toren, Dearing*, & *Shevock* 7714 (CAS).

****Tortella fragilis* (W. J. Hooker & Wilson in Drummond) Limpricht** [Pottiaceae]

Illustrations: Abramov and Volkova 1998; Crum and Anderson 1981; Eckel 1991; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Saito 1975; Smith 1978; Zander 1993.

Geographic subdivisions: SN, SNE.

Selected specimens: Inyo Co.: above Robinson Lake south of Onion Valley, Inyo National Forest, *Norris* 46659 and east of Dragon Peak and north of Golden Trout Lake near Onion Valley, John Muir Wilderness, Inyo National Forest, *Norris* 46748 (confirmed by Eckel); Mono Co.: above Robinson Lake on trail to Barney Lake southeast of Twin Lakes, Toiyabe National Forest, *Norris* 99649.

***Tortella tortuosa* (Hedwig) Limpricht**

[Pottiaceae]

Literature: Spjut 1971.**Illustrations:** Abramov and Volkova 1998; Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994; Smith 1978; Zander 1993.**Geographic subdivisions:** CaR, NW, SNE.**Selected specimens:** Alpine Co.: Noble Canyon Trail near junction with Pacific Crest Trail, Toiyabe National Forest, *Norris 99691*; Fresno Co.: canyon above Boyden Cave, Monarch Wilderness, Sequoia National Forest, *Shevock & York 13617*; Mono Co.: Convict Creek above Convict Lake, Inyo National Forest, *Shevock 13792*; Shasta Co.: Fall Creek Road about 1 mile southeast of McCloud Bridge at Shasta Lake, Shasta-Trinity National Forest, *Norris 84880* and Highway 299 at Oak Run Road, *Norris 80315 & 80336*; Siskiyou Co.: near Echo Lake north of Red Butte about 5 air miles north of Seiad Valley, Klamath National Forest, *Spjut 1057* (UC) and *Norris 57607*.***Tortula atrovirens* (J. E. Smith) Lindberg**

[Pottiaceae]

Literature: Kellman 2003; Millsbaugh and Nuttall 1923; Shevock and Toren 2001. As *Barbula atrovirens* Watson 1880. As *Desmatodon californicus* Lesquereux 1868. As *Desmatodon convolutus* Flowers 1973; Harpel 1980a; Harthill et al. 1979; Koch 1950a; Koch and Ikenberry 1954; McCleary 1972; Sayre 1940; Sigal 1975; Spjut 1971; Steere 1954; Toren 1977; Yurky 1990, 1995. As *Desmatodon nervosus* Kingman 1912. As *Desmatodon nervosus* var. *edentulus* Brandegee 1891; Lesquereux 1868; Lesquereux and James 1884.**Illustrations:** Flowers 1973; Smith 1978; Zander 1993.**Geographic subdivisions:** CW, DMoj, DSon, SN, SW.**Selected specimens:** Imperial Co.: about 2 miles east of Mountain Springs County Park, Colorado Desert, *Norris & Piippo 82087* (determined by Delgadillo); Inyo Co.: mouth of Grapevine Canyon, Death Valley National Park, *Norris 10217a* (determined by Crum); Kern Co.: Highway 178, Lower Kern River Canyon at Richbar, Sequoia National Forest, *Shevock & Tan 13035*; Lake Co.: Hell's Peak, *Toren 649* (SFSU, UC); Orange Co.: Mojessa Canyon near Tucker Bird Sanctuary, Cleveland National Forest, *Shevock 4001*; San Luis Obispo Co.: Highway 166 at Clear Creek, Los Padres National Forest, *Norris 80633* (determined by Delgadillo); Santa Barbara Co.: Windmill Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock 20766* (determined by Delgadillo).***Tortula brevipes* (Lesquereux) Brotherus**

[Pottiaceae]

Literature: Flowers 1973; Harpel 1980a; Harthill et al. 1979; Kingman 1912; Koch 1950a; Koch andIkenberry 1954; Lawton 1971; McCleary 1972; Mishler 1978; Shevock and Toren 2001; Steere 1954; Toren 1977. As *Barbula brevipes* Brandegee 1881; Lesquereux 1868; Watson 1880. As *Barbula macrotricha* Cardot and Thériot 1904.**Illustrations:** Flowers 1973; Lawton 1971; Sharp et al. 1994.**Geographic subdivisions:** CW, DMoj, DSon, GV, MP, NW, SN.**Selected specimens:** Alameda Co.: on concrete retaining wall, Berkeley, *Cook 1* (UC); Colusa Co.: Highway 20 at milepost 74, *Norris 52511*; Imperial Co.: about 2 miles east of Mountain Springs County Park, *Norris & Piippo 82106*; Lake Co.: Highway 20 at New Long Valley Road, *Toren 7301* (CAS); Modoc Co.: vicinity of Hot Springs north of Middle Alkali Lake northeast of Cedarville, *Norris 47483*; Tulare Co.: north of Three Rivers just below Sequoia National Park boundary, *Shevock & Morosco 16765*.***Tortula californica* E. B. Bartram** [Pottiaceae]**Literature:** Bartram 1945; Harthill et al. 1979; Koch 1950a; McCleary 1972; Steere 1954.**Illustrations:** Bartram 1945; Sharp et al. 1994.**Geographic subdivisions:** CW, GV, MP, SW.**Selected specimens:** Kern Co.: Hart Park east of Bakersfield, *Norris 50749*; Modoc Co.: about 9 miles east of Cedarville along Highway 299, *Norris 47462*; Monterey Co.: Highway 1 near milepost 65.02, Garrapata State Park, *Kellman 2954* (CAS); Riverside Co.: Lower Decker Canyon, Elsinore Mountains, *Fosberg 307* (LAM); San Diego Co.: Santa Margarita Ecological Reserve, between Temecula and Fallbrook, *Kellman 1392* (CAS) [determined by Mishler]; Santa Barbara Co.: Cherry Canyon, Santa Rosa Island, Channel Islands National Park, *Shevock 20913*.***Tortula euryphylla* Zander** [Pottiaceae]**Literature:** As *Desmatodon latifolius* Harthill et al. 1979; Koch 1950a, 1951e; Lawton 1971; Lesquereux 1868; McGrew 1976; Mishler 1978; Showers 1982; Spjut 1971; Strid 1974. As *Desmatodon latifolius* var. *muticus* Koch 1958; Lesquereux 1868; Watson 1880.**Illustrations:** Ignatov and Ignatova 2003. As *Desmatodon latifolius* Crum and Anderson 1981.**Geographic subdivisions:** CaR, NW, SN, SNE.**Selected specimens:** Inyo Co.: Chocolate Lake west of Big Pine, John Muir Wilderness, Inyo National Forest, *Norris 46898* and Horseshoe Meadows Road near Little Cottonwood Creek, Inyo National Forest, *Shevock & Ng 17593*; Siskiyou Co.: Big Duck Lake, Klamath National Forest, *Norris 23356*; Tulare Co.: Mineral King on trail to Sawtooth Pass, Sequoia National Park, *Shevock & O'Brien 16032*.***Tortula guepinii* (Bruch & W. P. Schimper)****Brotherus** [Pottiaceae]**Literature:** As *Barbula guepini* Watson 1880. As *Desmatodon guepinii* Harthill et al. 1979; Kingman

1912; Koch 1950a; Koch and Ikenberry 1954; Lesquereux 1868; Lesquereux and James 1884; McCleary 1972; Millspaugh and Nuttall 1923; Steere 1954; Toren 1977; Whittemore and Sommers 1999.

Illustrations: Sharp et al. 1994.

Geographic subdivisions: CW, DSon, NW, SN, SW.

Selected specimens: Alameda Co.: Oakland, *Bolander* 47 (UC); Contra Costa Co.: Pine Canyon near Castle Rocks, Mt. Diablo State Park, *Norris* 100793; Kern Co.: Highway 178 about 0.7 mile east of Chimney Peak Road, *Shevock & Tan* 13073; Lake Co.: Manning Creek, Highway 175 about 4 miles west of Lakeport, *Toren, Bourell, Dearing, & Shevock* 6997 (CAS); San Benito Co.: Logs Path from Park Headquarters to High Peaks, Pinnacles National Monument, *Koch* 3720 (UC); San Diego Co.: Bow Willow Canyon Campground, Anza Borrego State Park, *Norris* 77742; Siskiyou Co.: Highway 96 about 2 miles from Fort Goff, *Norris* 72263; Tulare Co.: trail to waterfall near Stevenson Gulch, Middle Fork Tule River, Sequoia National Forest, *Shevock & Tan* 13108.

***Tortula inermis* Bridel [Pottiaceae]**

Literature: Coville 1893; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Koch 1950a; Lawton 1971; Long 1978; Mishler 1978; Strid 1974; Werger and During 1989. As *Barbula inermis* Lesquereux 1868; Lesquereux and James 1884; Watson 1880.

Illustrations: Flowers 1973; Lawton 1971; Sharp et al. 1994.

Geographic subdivisions: CW, DMoj, DSon, GV, NW, SN, SNE, SW.

Selected specimens: Fresno Co.: Warthan Creek about 7 miles west-southwest of Coalinga, *Norris* 55128; Kern Co.: Erskine Creek Canyon about halfway between Lake Isabella Blvd. and Liebel Ranch, Piute Mountains, *Shevock* 13358; Lake Co.: Mt. Konocti, shore of Clear Lake at Soda Bay, *Toren* 7167 (CAS) [determined by Mishler]; Riverside Co.: between Key Ranch and Barker Dam, Joshua Tree National Park, Mojave Desert, *Norris* 50523; Tehama Co.: end of Buckhorn Road, Black Butte Recreation Area, *Norris & Piippo* 82373; Trinity Co.: Swede Rock along Trinity River, Shasta-Trinity National Forest, *Norris* 51102.

****Tortula leucostoma* (R. Brown) W. J. Hooker & Greville [Pottiaceae]**

Illustrations: As *Desmatodon leucostoma* Lawton 1971.

Geographic subdivisions: CaR, MP.

Selected specimens: Modoc Co.: Highway 139 at Biles Road about 13 miles northwest of Canby, *Norris* 70480; Tehama Co.: Howard Creek trail about 1 mile east of Highway 299, *Norris* 55496 and Highway 36 east of Red Bluff at Mile Creek, *Norris* 21243.

***Tortula mucronifolia* Schwägrichen [Pottiaceae]**

Literature: Harpel 1980a; Harthill et al. 1979; Koch 1950a; Showers 1982; Strid 1974; Toren 1977.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971; Sharp et al. 1994; Zander 1993.

Geographic subdivisions: CaR, MP, NW, SN, SW.
Selected specimens: Modoc Co.: along Highway 299 about 2 miles east of Middle Lake, *Norris* 70424; Riverside Co.: road below Pine Cove, San Jacinto Mountains, San Bernardino National Forest, *Harpel* 1237 (pers. herb.); Trinity Co.: Highway 299 about 4 miles west of Weaverville, *Norris* 73507; Tulare Co.: John Muir Trail at Wallace Creek, Sequoia National Park, *Peterson* 34 (UC).

***Tortula muralis* Hedwig [Pottiaceae]**

Literature: Crum and Anderson 1981; Harpel 1980a; Harthill et al. 1979; Howe 1896; Kellman 2003; Kingman 1912; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Shevock and Toren 2001; Showers 1982; Steere et al. 1954; Toren 1977; Yurky 1990, 1995.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Lawton 1971; Smith 1978.

Geographic subdivisions: CaR, CW, MP, NW, SW.
Selected specimens: Humboldt Co.: on brick of house, Lewis Avenue and 11th Street, Arcata, *Norris* 8295; Lassen Co.: Highway 139 about 16 miles south of Adin, *Norris* 21459; Modoc Co.: vicinity of Hot Spring north of Middle Alkali Lake northeast of Cedarville, *Norris* 47506; Riverside Co.: Forest Road 5S09 along tributary of Stone Creek, San Jacinto Mountains, San Bernardino National Forest, *Harpel* 1189 (pers. herb.); San Francisco Co.: Golden Gate Park, San Francisco, *Shevock* 18904; Shasta Co.: along County Road A17 at intersection to Black Butte, *Norris* 23751.

***Tortula obtusifolia* (Schwägrichen) Mathieu [Pottiaceae]**

Literature: Kellman 2003; Shevock and Toren 2001. As *Desmatodon avenaceus* Kingman 1912. As *Desmatodon obtusifolius* Crum and Anderson 1981; Flowers 1973; Koch 1950a; Lesquereux and James 1884; Showers 1982.

Illustrations: Crum and Anderson 1981; Flowers 1973; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971.

Geographic subdivisions: CaR, CW, GV, NW, SN, SNE.

Selected specimens: Contra Costa Co.: Pine Canyon, Mt. Diablo State Park, *Norris* 100788; Inyo Co.: above Treasure Lake west of Big Pine, Inyo National Forest, *Norris* 46972; Lake Co.: Manning Creek, Highway 175 about 4 miles west of Lakeport, *Toren, Bourell, Dearing, & Shevock* 6998 (CAS); Monterey Co.: bluffs at the Pinnacles, Hunter-Liggett Military Reservation, *Norris* 87313;

Shasta Co.: Interstate 5 about 3 miles north of Tehama County line, *Norris* 48221; Tehama Co.: Highway 36 about 5 miles northeast of Red Bluff, *Norris* 48078; Tulare Co.: Bear Creek Road north of Scicon, Sequoia National Forest, *Shevock* 3971.

***Tortula plinthobia* (Sullivant & Lesquereux in A. Gray) Brotherus [Pottiaceae]**

Literature: Shevock and Toren 2001. As *Desmatodon plinthobius* Harpel 1980a; Harthill et al. 1979; Kingman 1912.

Illustrations: As *Desmatodon plinthobius* Crum and Anderson 1981; Flowers 1973.

Geographic subdivisions: CW, DMoj, MP, SW.

Selected specimens: Modoc Co.: Highway 299 about 2 miles east of Middle Lake, *Norris* 70423; Riverside Co.: Snow Creek Canyon, Desert Water Agency, *Harpel* 1160 (pers. herb.); San Francisco Co.: Third Street and Burke Street, San Francisco, *Shevock* 20206; San Luis Obispo Co.: Highway 58 about 1 mile east of La Panza Ranch, Los Padres National Forest, *Norris* 76290.

***Tortula protobryoides* Zander [Pottiaceae]**

Literature: As *Pottia bryoides* Harthill et al. 1979; Koch 1950a; Lesquereux 1868; McCleary 1972; Steere 1954. As *Mildeella bryoides* Howe 1897.

Illustrations: Arts 1987; Ignatov and Ignatova 2003; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CW, NW, SW.

Selected specimens: Alameda Co.: Brushy Peak northeast of Livermore, *Norris* 87174; Lake Co.: Highway 53 about 1 mile south of Highway 20, *Norris* 47705; Los Angeles Co.: San Gabriel Canyon, *MacFadden* 16879 (MO), La Tuna Canyon, Verdugo Hills, *MacFadden* 8115 (MO), and San Clemente Island, *Wheeler* 8088 (CAS, UC); Monterey Co.: Sam Jones Road about 1 km east of Pajojo Airstrip, Hunter-Liggett Military Reservation, *Norris* 87264; Riverside Co.: Santa Margarita River, *Kellman* 1379a (CAS) [determined by Stark]; San Diego Co.: San Vicente Dam about 3 miles north of Lakeside, *Stark* 692 (MO).

***Tortula subulata* Hedwig [Pottiaceae]**

Literature: Harthill et al. 1979; Holmberg 1969; Kellman 2003; Koch 1950a, 1951e; Koch and Ikenberry 1954; Lawton 1971; Mishler 1978; Showers 1982; Spjut 1971; Steere et al. 1954; Toren 1977. As *Barbula subulata* Lesquereux 1868; Watson 1880. As *Tortula angustata* Howe 1897.

Illustrations: Ignatov and Ignatova 2003; Lawton 1971; Smith 1978; Zander 1993.

Geographic subdivisions: CaR, CW, MP, NW, SN.

Selected specimens: Lake Co.: Cobb Mountain east of Geyser Rock, *Toren & Dearing* 7085 (CAS); Mariposa Co.: Summit Road about 2 miles north of Fish Camp, Sierra National Forest, *Norris* 85353; Modoc Co.: Highway 89 at Bear Creek, *Norris* 77940; Santa Cruz Co.: Eagle Rock, *Kellman* 886 (CAS); Shasta Co.: Lost Creek near Boundary Spring, Lassen Volcanic National Park,

Showers 2220 (UC); Siskiyou Co.: about 1 mile east of Copper Butte, *Norris* 50243; Tehama Co.: South Fork Beegum Creek about 1.5 miles west of Rat Trap Gap, *Norris* 56978; Tulare Co.: Forest Trail 31E18 at Silver Creek, Sequoia National Forest, *Shevock* 9082.

***Tortula systylia* (W. P. Schimper) Lindberg [Pottiaceae]**

Literature: As *Desmatodon systylius* Koch 1950a; Lesquereux 1868; Lesquereux and James 1884; Watson 1880.

Illustrations: As *Desmatodon systylius* Crum and Anderson 1981; Lawton 1971.

Geographic subdivisions: SN.

Selected specimens: Tulare Co.: Kern Plateau, along road 4.2 miles north of BLM Long Valley Campground and 6.7 miles southwest of Kennedy Meadows Road, *Shevock, Ng, & Markos* 18306.

****Tortula truncata* (Hedwig) Mitten in Godman [Pottiaceae]**

Illustrations: Zander 1993. As *Pottia truncata* Crum and Anderson 1981; Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: DMoj.

Selected specimens: Los Angeles Co.: Highway 138 about 3 miles west of Palmdale, *Norris* 68096.

***Trachybryum megaptilum* (Sullivant) W. B. Schofield [Brachytheciaceae]**

Literature: As *Camptothecium megaptilum* Howe 1897; Koch 1950a; Koch and Ikenberry 1954. As *Homalothecium megaptilum* Bourell 1981; Holmberg 1969; Lawton 1971; and McGrew 1976.

Illustrations: Lawton 1971.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: Del Norte Co.: Forest Road 4803, Siskiyou National Forest, *Norris* 70881; Humboldt Co.: road to Eight Mile Lookout about 1 mile west of South Fork Mountain Road, Six Rivers National Forest, *Norris* 83857; Lake Co.: near Violet Spring, Mendocino National Forest, *Toren* 7435 & 7455 (CAS); Mendocino Co.: East Side Road at Knight Hill along Russian River about 8 miles south of Ukiah, *Norris* 72642; Plumas Co.: about 0.5 mile south of Snake Lake and 4 miles northwest of Quincy, Plumas National Forest, *Dillingham* 925 (CAS); Shasta Co.: Highway 299 about 1 mile north of Mineral School at road intersection to Oak Run, *Norris* 68632; Siskiyou Co.: south of Seattle Bar, Rogue River National Forest, *Shevock & Toren* 20090 and McCloud River Preserve, The Nature Conservancy, *Norris & Hillyard* 106584.

****Trematodon boasii* W. B. Schofield [Bruchiaceae]**

Illustrations: Schofield 1966c.

Geographic subdivisions: SN.

Selected specimens: Sierra Co.: Highway 49 at

Yuba Pass, Tahoe National Forest, *Kellman* 251 (UC).

****Trichodon cylindricus* (Hedwig) W. P. Schimper** [Ditrichaceae]

Illustrations: Crum and Anderson 1981; Ireland 1978, 1982; Seppelt 1999.

Geographic subdivisions: CaR, NW.

Selected specimens: Humboldt Co.: near Scotty Point south of Patricks Point off of Highway 1, *Norris* 72937; Lake Co.: north cirque of Hull Mountain, Mendocino National Forest, *Toren & Dearing* 7616 (CAS) [confirmed by Ireland]; Mendocino Co.: Mt. Sanhedrin south of Little Signal Peak, *Toren, Heise, & Dearing* 7622 (CAS); Siskiyou Co.: below Castle Lake at campground site, Shasta-Trinity National Forest, *Toren & Shevock* 8188 (CAS).

****Trichostomum brachydontium* Bruch in F. A. Mueller** [Pottiaceae]

Illustrations: Allen 2002; Smith 1978.

Geographic subdivisions: SNE.

Selected specimens: Inyo Co.: end of Big Pine Creek Road near Glacier Lodge, Inyo National Forest, *Laeger* 1432 (CAS, MO).

****Trichostomum crispulum* Bruch in F. A. Mueller** [Pottiaceae]

Illustrations: Allen 2002; Ignatov and Ignatova 2003; Smith 1978; Zander 1993.

Geographic subdivisions: DMoj, NW.

Selected specimens: Humboldt Co.: Redwood Valley Road about 2 miles north of Redwood Valley, *Norris* 21222; Inyo Co.: South Fork Hanaupah Canyon, east base of Telescope Peak, Death Valley National Park, *Shevock & York* 21343; San Bernardino Co.: Coyote Canyon, Granite Mountains, Mojave National Preserve, *Norris* 87853.

****Trichostomum sweetii* (E. B. Bartram) Stark** [Pottiaceae]

Illustrations: Bartram 1945.

Geographic subdivisions: CW, DMoj, DSON.

Selected specimens: Contra Costa Co.: Mitchell Canyon, Mt. Diablo State Park, *Norris* 100613; Madera Co.: East Fork Chowchilla River, *Norris* 51068; Riverside Co.: eight miles west of Desert Center on road toward Twenty Nine Palms, Mojave Desert, *Norris* 57914; San Bernardino Co.: Interstate 15 at Zzyzx, *Bonine* 737 (UNLV) [determined by Stark].

***Tripterocladium leucocladulum* (C. Müller Hal.) A. Jaeger** [Hypnaceae]

Literature: Christy and Wagner 1996; Crum 1987; Koch 1950a; Lawton 1971.

Illustrations: Brothaus 1924–1925; Lawton 1971.

Geographic subdivisions: NW.

Selected specimens: Siskiyou Co.: Beaver Creek, south of junction of West Fork Beaver Creek, *Ownbey & Ownbey* 1897 (CAS).

***Triquetrella californica* (Lesquereux) Grout** [Pottiaceae]

Literature: Christy and Wagner 1996; Koch 1949a, 1950a; Shevock and Toren 2001; Stark 1980; Yurky 1995. As *Anomodon californicum* Lesquereux 1868.

Illustrations: Casas et al. 1993; Zander 1993.

Geographic subdivisions: CW, NW, SW.

Selected specimens: Contra Costa Co.: Mount Diablo, *Bolander* 203 (NY); Del Norte Co.: along Requa Trail, Redwood National Park, *Norris* 24103; Marin Co.: near Olema, Point Reyes National Seashore, *Howe* 30 (NY); Mendocino Co.: MacKerricher State Park, *Norris* 8533 (and CAS); San Diego Co.: slopes of San Vicente Reservoir midway between San Vicente Dam and south entrance parking lot, about 3 miles north of Lakeside, *Stark* 540d, 584, & 684 (MO); San Francisco Co.: Tank Hill, Clarendon Heights, *Shevock* 18920 (confirmed by Zander) and Clipper Street at Douglas Playground, *Toren* 7778 (CAS); Sonoma Co.: near Bodega Marine Laboratory, *Norris* 103485.

***Ulota megalospora* Venturi in Röll** [Orthotrichaceae]

Literature: Christy and Wagner 1996.

Illustrations: Grout 1928–1940; Lawton 1971.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: Gasquet-Oreans Road about 6.5 miles from Big Flat, Six Rivers National Forest, *Norris* 74144 & 74145; Humboldt Co.: near French Camp, *Norris* 24304 and Forest Road 10N02 at head of Mill Creek, Six Rivers National Forest, *Norris* 70593; Siskiyou Co.: trail from Wilderness Falls toward Doe Flat, Klamath National Forest, *Norris* 67815; Trinity Co.: Onion Lake Road about 7 miles south of Onion Lake, Shasta-Trinity National Forest, *Norris & Rivera* 72572.

****Ulota obtusiuscula* C. Müller Hal. & Kindberg in Macoun** [Orthotrichaceae]

Illustrations: Ireland 1982; Smith 1978.

Geographic subdivisions: NW.

Selected specimens: Del Norte Co.: French Hill Road about 2.5 miles above Highway 199, southwest of Gasquet, Six Rivers National Forest, *Norris* 85050 and Little Rattlesnake Mountain, Six Rivers National Forest, *Wheeler* 7390 (UC); Humboldt Co.: Blue Lake near Weitchpec, *Norris* 56340 and 2 miles south of the mouth of Mad River, *Norris* 7660; Trinity Co.: Highway 36 at Olsen Creek, Six Rivers National Forest, *Norris* 56631.

***Ulota phyllantha* Bridel** [Orthotrichaceae]

Literature: Koch 1949a, 1950a.

Illustrations: Ireland 1982; Lawton 1971; Smith 1978.

Geographic subdivisions: CW, NW.

Selected specimens: Del Norte Co.: Kellogg Beach State Park at end of Pala Road west of Smith River,

Norris 75029; Humboldt Co.: College Cove about 2 miles north of Trinidad, *Norris 23621*, Ten Taypo Trail, Prairie Creek Redwood State Park, *Norris 56767*, and near Abalone Point, Patrick's Point State Park, *Norris 23880*; Marin Co.: coastal Headlands at Point Reyes Lighthouse, Point Reyes National Seashore, *Robertson 1144* (UC) and Pierce Point Road, Point Reyes National Seashore, *Robertson 1920* (CAS); Mendocino Co.: Inglenook Fen north of Fort Bragg, *Norris 23433* and *Norris 68777*.

***Vesicularia vesicularis* (Schwägrichen)**

Brotherus [Hypnaceae]

Literature: Shevock and Toren 2001. As *Vesicularia amphibola* Koch 1949a, 1950a.

Illustration: Sharp et al. 1994.

Notes: This species is an introduced component of the California moss flora.

Geographic subdivisions: CW.

Selected specimens: San Francisco Co.: Golden Gate Park, Conservatory, *Toren 688* (CAS, SFSU), *Bradshaw s.n.* (CAS), and *Wagner s.n.* (CAS).

***Warnstorfia exannulata* (W. P. Schimper in B.S.G.) Loeske** [Campyliaceae]

Literature: As *Drepanocladus exannulatus* Ireland 1982; Koch 1950a, 1958; Koch and Ikenberry 1954; Lawton 1971; McGrew 1976; Showers 1982; Spjut 1971; Wynne 1944. As *Harpidium exannulatum* Cooke 1941. As *Hypnum exannulatum* var. *cochleae* Watson 1880.

Illustrations: Flowers 1973; Hedenäs 1987, 1993a, 2003; Ireland 1982; Janssens 1983; Kanda 1978; Koponen et al. 1995; Lawton 1971; Smith 1978; Wynne 1944.

Geographic subdivisions: CaR, NW, SN.

Selected specimens: El Dorado Co.: Grass Lake west of Luther Pass, Eldorado National Forest, *Norris 71308*; Fresno Co.: Taboose Pass Trail, Kings Canyon National Park, *Shevock 13861*; Lassen Co.: Aspen Grove Campground, south end of Eagle Lake, Lassen National Forest, *Norris 52820*; Siskiyou Co.: South Sugar Lake, Klamath National Forest, *Norris & McGrew 45637*; Tuolumne Co.: near Piute Meadow, Emigrant Wilderness, Stanislaus National Forest, *Norris 77099*.

***Warnstorfia fluitans* (Hedwig) Loeske** [Campyliaceae]

Literature: As *Drepanocladus fluitans* Ireland 1982; Janssens 1983; Koch 1950a, 1951e, 1958; McGrew 1976; Spjut 1971; Toren 1977; Wynne 1944. As *Dichelyma swartzii* Lesquereux 1868.

Illustrations: Flowers 1973; Hedenäs 1993a; Ireland 1982; Janssens 1983; Kanda 1978; Koponen et al. 1995; Lawton 1971; Smith 1978; Wynne 1944.

Geographic subdivisions: MP, NW, SN.

Selected specimens: Alpine Co.: Highway 89 at Hope Valley, Toiyabe National Forest, *Norris 48476*; Glenn Co.: Keller Lake, west slope of Black

Butte, Mendocino National Forest, *Toren & Nilles 98-219* (CAS); Humboldt Co.: Snow Camp Lake, *Norris 50378*; Mendocino Co.: Pygmy Cypress Forest along County Road 409 about 1 mile east of Highway 1 south of Fort Bragg, *Norris 11758*; Modoc Co.: near Hager Reservoir, *Norris, Nelson, & Dowty 19422*; Tulare Co.: Mitre Basin, Sequoia National Park, *J.T. Howell s.n.* (CAS) and above Priam Lake, *J.T. Howell s.n.* (CAS).

***Weissia andersoniana* Zander** [Pottiaceae]

Literature: As *Weissia glauca* Harpel 1980a.

Illustrations: Sharp et al. 1994; Stoneburner 1981.

Geographic subdivisions: DMoj, DSon, SW.

Selected specimens: Inyo Co.: south of Towne Pass, Death Valley National Park, *Kellman, Shevock, & York 1427* (CAS); Riverside Co.: Snakeeye Springs, Indian Cove, Joshua Tree National Park, *Norris 57987* and Highway 74 at eastern boundary of San Bernardino National Forest, *Norris 57870*.

****Weissia andrewsii* E. B. Bartram** [Pottiaceae]

Illustrations: Sharp et al. 1994.

Geographic subdivisions: DMoj, DSon.

Selected specimens: Inyo Co.: Panamint City, Panamint Mountains, Death Valley National Park, *York, Laeger, & Knaus 2491* (CAS); Riverside Co.: Joshua Tree National Park, Snakeeye Springs, Indian Cove, *Norris 57986 & 57989*; and 5 miles south of road intersections to Salton View and Twenty Nine Palms, *Norris 50549*.

****Weissia condensata* (Voit in J. W. Sturm)**

Lindberg [Pottiaceae]

Illustrations: Allen 2002; Sharp et al. 1994.

Geographic subdivisions: DMoj, DSon, NW, SN.

Selected specimens: Lake Co.: Highway 29 about 1 mile north of Middletown, *Toren & Dearing 7305* (CAS) [determined by Stoneburner]; San Bernardino Co.: Coyote Canyon, Granite Mountains, Mojave National Preserve, *Norris 87859* and summit ridge of Chemechuevi Peak, Chemechuevi Mountains, *Laeger 640* (CAS); Siskiyou Co.: Scott River about 8 miles west of Fort Jones, *Norris 58190*; Tulare Co.: Sequoia National Park: Kaweah River near Clough Cave, *Norris & Shevock 92743* and Yucca Point Trail near Ash Mountain Park Headquarters, *Shevock & Whitmarsh 16995*.

***Weissia controversa* Hedwig** [Pottiaceae]

Literature: Bourell 1981; Crum and Anderson 1981; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Jamieson 1969; Kellman 2003; Koch 1950a, 1951e, 1958; Koch and Ikenberry 1954; Lawton 1971; McCleary 1972; Mishler 1978; Shevock and Toren 2001; Showers 1982; Sigal 1975; Strid 1974; Toren 1977; Whittemore and Sommers 1999; Yurky 1990, 1995. As *Weissia viridula* Brandege 1891; Kingman 1912; Lesquereux 1868; Steere 1954; Steere et al. 1954; Sullivant 1856; Watson 1880.

Illustrations: Allen 2002; Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982;

Lawton 1971; Sharp et al. 1994; Smith 1978; Stoneburner 1981; Zander 1993.

Geographic subdivisions: CW, MP, NW, SN, SW.

Selected specimens: Del Norte Co.: between Requa and False Klamath Cove, Redwood National Park, *Norris* 24048; Lassen Co.: Highway 138 about 3 miles north of Susanville, *Norris* 52793; Marin Co.: junction of Bolinas-Fairfax Road and Highway 1, Golden Gate National Recreation Area, *Yurky* 677 (SFSU); Riverside Co.: El Cariso Campground, Cleveland National Forest, *Norris* 58095; Trinity Co.: New River between Denny and Mills Creek, *Norris* 23941; Tulare Co.: Forest Trail 33E20 toward the Forks of the Kern River, Golden Trout Wilderness, Sequoia National Forest, *Shevock* 14269.

***Weissia inoperculata* (H. Crum) H. Crum, W. C. Steere & L. E. Anderson** [Pottiaceae]

Literature: As *Hymenostomum inoperculatum* Andrews 1924; Crum 1957.

Illustrations: Crum 1957.

Geographic subdivisions: CaR, CW, GV, NW.

Selected specimens: Santa Clara Co.: Stanford University Campus at Sequoia Hall, *Schofield* s.n. (CAN) [determined by Crum]; Shasta Co.: Anderson to Shingletown Road about 11 miles east of Anderson, *Norris* 23707, Brushy Oak Trail at Oak Run Creek east of Highway 299, *Norris* 80372 and Highway 299 about 9 miles east of Bella Vista, *Norris* 47622; Trinity Co.: Hall City Caves east of Wildwood, Shasta-Trinity National Forest, *Norris* 71667.

***Zygodon menziesii* (Schwägrichen) Arnott** [Orthotrichaceae]

Literature: Shevock 2000; Shevock and Toren 2001.

Illustrations: Catcheside 1980; Lewinsky 1989.

Notes: This species has recently been transferred back into the genus *Codonoblepharon* Schwägrichen. See Crosby et al. 2000; Goffinet and Vitt 1998.

Geographic subdivisions: CW.

Selected specimens: San Francisco Co.: Panhandle, Golden Gate Park, *Shevock* 18773 and *Toren* 7797 (CAS), Jefferson Park, *Shevock* 18901 (confirmed by Vitt).

***Zygodon rupestris* W. P. Schimper ex Lorentz** [Orthotrichaceae]

Literature: Shevock and Toren 2001. As *Zygodon viridissimus* Crum 1957; Crundwell 1957; Harthill et al. 1979; Koch 1950b; Mishler 1978; Saito 1970; Thomson and Ketchledge 1958; Toren 1977. As *Zygodon viridissimus* var. *rupestris* Holmberg 1969; Jamieson 1969. As *Zygodon vulgaris* Bourell 1981; Lawton 1971.

Illustrations: Ignatov and Lewinsky-Haapasaaari 1994; Ireland 1981; Lawton 1971; Sharp et al. 1994; Smith 1978.

Geographic subdivisions: CW, NW, SN, SW.

Selected specimens: Calaveras Co.: South Fork

Mokelumne River between West Point and Railroad Flat, *Norris & Shevock* 103382; Del Norte Co.: Stony Creek about 1 mile north of junction with Smith River, *Norris* 52766 and west of Hiouchi Bridge, Jedediah Smith Redwoods State Park, *Norris* 67315; Humboldt Co.: Eel River about 3 miles north of the start of the Avenue of the Giants, *Norris* 72146; Los Angeles Co.: USFS San Dimas Experimental Forest, Angeles National Forest, *Mishler* s.n. (LAM); Mendocino Co.: Ornbaun Creek near Mountain View Road, *Norris* 53210; San Francisco Co.: St. Francis Blvd., San Francisco, *Toren* 5001 (CAS); Santa Cruz Co.: San Lorenzo River near Rincon Road, Henry Cowell Redwoods State Park, *Kellman* 669 (UC); Trinity Co.: Highway 299 at Big French Creek Campground west of Big Bar, Shasta-Trinity National Forest, *Norris* 46134.

APPENDIX II

EXCLUDED TAXA

Koch (1950a) provided a list of taxa at the end of each family entry that he considered as erroneous records for California. Several of these taxa have subsequently been documented from California with a voucher specimen. We have not transferred all of the remaining excluded records of Koch (1950a) to this section except in a few cases where we have additional information or comment. In some cases, a different circumscription or species concept required modifications to names that were used in earlier checklists of mosses for California.

***Bryum arcticum* (R. Brown) Bruch & W. P. Schimper** [Bryaceae]

Literature: Lesquereux 1868; Lesquereux and James 1884; Watson 1880.

Notes: We were unable to locate any historic packets to confirm this taxon in California. We have excluded it from the catalogue even though Lesquereux (1868) references a Bolander collection from Mt. Dana, Yosemite National Park.

***Callicladium haldanianum* (Greville) H. Crum** [Hypnaceae]

Literature: Lawton 1971.

Notes: Although attributed for California by Lawton (1971) no voucher is cited. The nearest documented collection that we have seen occurs in Arizona (MO).

***Campylium radicale* (Palisot de Beauvois) Grout** [Campyliaceae]

Literature: Spjut 1971.

Notes: The specimen attributed in Spjut's thesis we believe was misidentified since it could not be located at UC under this name. Apparently this collection has been annotated and filed elsewhere in the herbarium. None of the California *Campylium* specimens we examined is this species.

Campylopus pilifer* Bridel [Dicranaceae]*Literature:** Frahm 1980.**Notes:** Material originally attributed as this taxon in California has been re-named by Frahm as representing *Campylopus introflexus*. The nearest occurrence of *Campylopus pilifer* occurs in Arizona according to Frahm (1980).***Climacium dendroides* (Hedwig) Weber & D. Mohr [Climaciaceae]****Literature:** Flowers 1973.**Notes:** The reference to *Climacium* occurring in California is based on Flowers (1973). There is a very small fragment of *Climacium* at MO attributed for California and collected by MacFadden in 1957. However, it is not an original label and the locality is not clearly specified. This is extremely atypical for MacFadden collections and we are inclined to dismiss this record as a possible herbarium processing/labeling error. It is unlikely that collectors would have overlooked this species in California considering its large size and distinctive appearance, however, it is possible that it could be located within the state near the Oregon border. *Climacium dendroides* is documented from herbarium specimens in Oregon and to the east in Arizona. This taxon appears to be distributed throughout the mountainous western states except California and Nevada.***Didymodon luridus* Hornschush in Sprengel [Pottiaceae]****Literature:** Moxley 1928. As *Didymodon trifarius* Jamieson 1969; Koch 1950a. As *Didymodon vinealis* var. *luridus* Zander 1993.**Notes:** According to Zander, *Didymodon luridus* does not occur in California. Specimens attributed to this taxon in California are most likely within the *D. vinealis* complex.***Entodon brevisetus* (W. J. Hooker & Wilson) Lindberg [Entodontaceae]****Literature:** Harthill et al. 1979; Koch 1950a.**Notes:** This moss has not been subsequently rediscovered in California. We concur with Koch (1950a) that the original specimen was most likely a labelling error. We are inclined to dismiss this taxon as a component of the California moss flora. This record is based on a collection attributed from Los Angeles County near Pasadena, *McClatchie 12* (EGB).***Funaria americana* Lindberg in Sullivant [Funariaceae]****Literature:** Koch 1950a; Yurky 1990, 1995. Attributed to California by Jennings (1913) and Bartram (1928). See also Crundwell and Nyholm 1974; Smith 1980.**Notes:** Although attributed for California from several sources, we have not located a collection that we have determined to be this taxon in the state. We are of the opinion that these California recordsare merely misidentifications, presumably of *Funaria hygrometrica*.***Grimmia donniana* Smith [Grimmiaceae]****Literature:** Crum and Anderson 1981; Spjut 1971.**Notes:** Although reported for California in the literature, all of the California specimens we have examined have been misidentified. No specimens of this taxon have been determined by Muñoz as occurring in the state as part of his review of California *Grimmia* holdings at UC.***Grimmia incurva* Schwägrichen [Grimmiaceae]****Literature:** McGrew 1976; Spjut 1971. As *Grimmia contorta* Lesquereux 1868; Lesquereux and James 1884.**Notes:** Although reported for California for over a century, examination of specimens have not validated this taxon for California. According to Muñoz (personal communication), this taxon is unlikely to occur in California.***Grimmia involucrata* Cardot [Grimmiaceae]****Literature:** McCleary 1972.**Notes:** The specimen attributed as this taxon from the Channel Islands was determined by Muñoz to be *Grimmia lisae*. According to Muñoz, this taxon would be unlikely to occur in California.***Grimmia pilifera* Palisot de Beauvois [Grimmiaceae]****Literature:** Coville 1893. As *Grimmia arizonae* Koch 1950a. See also Muñoz and Pando 2000.**Notes:** Although attributed for California, we have not seen specimens to validate this species in the state. A Weber collection (COLO) from California labelled as *G. pilifera* has been determined by Muñoz as *G. lisae*. Muñoz and Hastings (personal communication) are both of the opinion that this species is not in California, however, Hastings does recognize *G. arizonae* as distinct from *G. pilifera*. The nearest confirmed occurrences for *G. pilifera* are in eastern Arizona.***Grimmia unicolor* W. J. Hooker in Greville [Grimmiaceae]****Literature:** Koch 1950a.**Notes:** Specimens so labelled for California are misidentified, generally being *G. ovalis*. We have not seen a California packet annotated by either Greven or Muñoz to represent this species in California.***Haplocladium microphyllum* (Hedwig) Brotherus [Leskeaceae]****Literature:** Harthill et al. 1979; Koch 1950a; McCleary 1972; Steere 1954. As *Hypnum calyptratum* Sullivant 1856. As *Thuidium microphyllum* Sayre 1940.**Notes:** *Haplocladium microphyllum* reported for California is based on a collection obtained from near Los Angeles on Santa Catalina Island [see Koch 1950a; Sayre 1940]. We were not able to lo-

cate this specimen to validate this entry. The nearest herbarium specimen that we were able to find of *Haplocladium microphyllum* occurs in Arizona. We therefore have excluded this taxon until it can be confirmed for California.

***Hedwigia ciliata* (Hedwig) Palisot de Beauvois**
[Hedwigiaceae]

Literature: Buck and Norris 1996; Koch 1950a; Steere et al. 1954.

Notes: Although frequently reported in the literature as a component of the California moss flora, the Californian material actually represents two different taxa. See narrative under *Hedwigia detonsa* and *Hedwigia stellata* in this catalogue.

***Hypnum cupressiforme* Hedwig** [Hypnaceae]

Literature: Koch 1950a; Yurky 1995.

Notes: The California record is based on a Marin County collection that we have not been able to locate and validate. Mt. Tamalpais, *Bailey s.n.* (Koch 1950a). *Hypnum cupressiforme* has proven to be a rather weedy species once introduced, especially in Hawai'i. If it becomes introduced to California, it would likely become a naturalized component of the state bryoflora in the coastal counties as a lawn weed.

***Mielichhoferia mielichhoferiana* (Funck) Loeske**
[Mielichhoferiaceae]

Literature: Shaw 1994a, 1994b.

Notes: The California material attributed as *Mielichhoferia mielichhoferiana* or *Mielichhoferia mielichhoferi* is *M. elongata*. See narrative under *Mielichhoferia elongata* in this catalogue.

***Pogonatum urnigerum* (Hedwig) Palisot de Beauvois** [Polytrichaceae]

Literature: Spjut 1971.

Notes: The specimen attributed in Spjut's thesis we believe was misidentified since it could not be located at UC under this name. Apparently it has been annotated and filed elsewhere in the herbarium, most likely to another member of the Polytrichaceae.

***Pohlia bulbifera* (Warnstorf) Warnstorf**
[Mniaceae]

Literature: Harpel 1980a; Harthill et al. 1979; Long 1978.

Notes: See Shaw (1981a) for narrative features separating *Pohlia bulbifera* from *P. camptotrachela* and *P. andrewsii*. We were unable to locate and verify a California collection for this species.

***Pohlia longicollis* (Hedwig) Lindberg** [Mniaceae]

Literature: Strid 1974.

Notes: The specimen cited in Strid's thesis as representing this taxon was not located. We were unable to locate and verify a California collection for this species and therefore have excluded it at this time.

***Pseudocrossidium revolutum* (Bridel in Schrader) Zander** [Pottiaceae]

Literature: Eckel 1997a.

Notes: *Pseudocrossidium revolutum* is currently viewed to be a Eurasian taxon and the western North American material is now treated as *Pseudocrossidium obtusulum* in this catalogue.

***Racomitrium aquaticum* (Bridel ex Schrader) Bridel** [Grimmiaceae]

Literature: Christy and Wagner 1996.

Notes: According to Dr. Halina Bednarek-Ochyra (2000), *Racomitrium aquaticum* has been erroneously attributed for the Pacific Northwest. The plants referred to this taxon from the Pacific Northwest (Lawton 1971) actually represent a new recently described species (*Racomitrium ryszardii*). Specimens previously identified as *R. aquaticum* from California represent other taxa.

***Racomitrium canescens* (Hedwig) Bridel**
[Grimmiaceae]

Literature: Bourell 1981; Crum and Anderson 1981; Flowers 1973; Howe 1897; Koch 1950a; Lesquereux 1868; Watson 1880; Yurky 1990, 1995.

Notes: Although reported for California in the literature, the California material represents *Racomitrium elongatum*, a taxon segregated from *R. canescens*.

***Rhizomnium nudum* (Britton & R. S. Williams) T. Koponen** [Mniaceae]

Literature: Christy and Wagner 1996.

Notes: Distribution map in Christy and Wagner (1996) displays range into California, however, no collections of this species have been located even after extensive surveys.

***Schistidium apocarpum* (Hedwig) Bruch & W. P. Schimper** [Grimmiaceae]

Literature: As *Grimmia apocarpa* Bourell 1981; Crum and Anderson 1981; Flowers 1973; Harpel 1980a; Harthill et al. 1979; Holmberg 1969; Howe 1896; Koch 1950a; Koch and Ikenberry 1954; Lawton 1971; Lesquereux 1868; Long 1978; McGrew 1976; Mishler 1978; Showers 1982; Sigal 1975; Spjut 1971; Steere et al. 1954; Toren 1977; Watson 1880. Misidentified as *Grimmia apocarpa* var. *atrofusca* McCleary 1972.

Notes: According to Hans Blom (1996), *Schistidium apocarpum*, common in northern Europe, has been misapplied to accommodate California collections. *Schistidium apocarpum* in North America is restricted to the extreme northeastern portion of the continent (Blom 1996). In California, the collections previously labelled as *Schistidium apocarpum* represent at least two undescribed species.

***Schistidium heterophyllum* (Kindberg in Macoun) McIntosh in L. E. Anderson, H. Crum & W. R. Buck** [Grimmiaceae]

Literature: As *Grimmia heterophylla* Toren 1977; Toren and Sigal 1974.

Notes: Literature references for this taxon in California are based on collections that have subsequently been determined to be *Grimmia tergestina*.

***Splachnum melanocaulon* (Wahlenberg)
Schwägrichen** [Splachnaceae]

Literature: Lesquereux 1868.

Notes: Habitat available for this species is attributed to California as indicated by Mitten in Lesquereux (1868). However, there are no herbarium specimens for this taxon occurring in California. Based on the current distribution for this species, it would be highly unlikely for this species to occur in California. We have therefore excluded it from the California moss flora.

***Syntrichia intermedia* Bridel** [Pottiaceae]

Literature: As *Tortula intermedia* McCleary 1972.

Notes: This species is excluded from Mishler's dissertation (1984) as occurring in California. The references to this taxon obtained from the Channel Islands is in error. However, we have not been able to review specimens so labeled to determine the correct placement in this catalogue.

***Tetraphis geniculata* Girgensohn ex Milde**
[Tetraphidaceae]

Literature: Christy and Wagner 1996.

Notes: Christy and Wagner (1996) report a California occurrence for *Tetraphis geniculata*, however, we have not confirmed the report with a voucher specimen. *Tetraphis pellucida* is confirmed for California. However, both species are known to occur in mixed populations in the Pacific Northwest. While we have excluded this species, it is still possible that it will be documented for California.

***Tortula fragilis* (Taylor) Ochyra** [Pottiaceae]

Literature: Harthill et al. 1979; Long 1978.

Notes: According to Mishler (personal communication) the earlier literature citations for this taxon as part of the California bryoflora are in error. The specimens originally attributed as *Tortula fragilis* most likely belong to *Tortula inermis* (*Syntrichia inermis* in this catalogue) and related species. *Tortula fragilis* is known from Mexico with the nearest U.S. occurrence being in the state of New Mexico. See also Mishler 1984.

APPENDIX III

POSSIBLE ADDITIONS TO THE CALIFORNIA MOSS FLORA

Several mosses documented in adjacent states (primarily Oregon) are expected to occur in California based on our assessment of similar habitats and vegetation types. In this Appendix we list those species where herbarium specimens have verified an occurrence basically within 50 air miles of the California border. We view these taxa as likely to be located in the state with ongoing field study and collection. We provide this list of likely new state

additions here in the expectation that other collectors will locate a California occurrence in the near future.

***Dicranoweisia crispula* (Hedwig) Milde**
[Seligeriaceae]

Notes: Although reported in the literature for the state, all of the California material attributed to this taxon have been determined by us to represent *D. contermina*. A recent collection along the Nevada side of Lake Tahoe we believe to be *D. crispula*. This species should be expected on the California side of the Lake Tahoe Basin.

Illustrations: Crum and Anderson 1981; Flowers 1956.

Selected specimens: NEVADA: Douglas Co.: along Highway 28 about 0.5 mile north of junction with Highway 50 just east of Lake Tahoe, *Shevock* 22061.

***Didymodon nevadensis* Zander in Zander, Stark & Marrs-Smith** [Pottiaceae]

Literature: Zander et al. 1995.

Illustrations: Zander et al. 1995.

Notes: Although this species is currently not recorded for California, it was originally described from populations near Las Vegas on gypsum soils. Since suitable habitat for this species occurs in the Death Valley region, this species could eventually be located in the state.

Selected specimens: NEVADA: Clark Co.: Lime Ridge about 16 km north of Gold Butte, *Stark & Marrs-Smith* NV-225a (UNLV) and Bitter Ridge, 1.2 km north of Black Butte, *Stark* NV-479 (UNLV).

***Hypnum revolutum* (Mitten) Lindberg var.
ravaldii (Boulay) Ando** [Hypnaceae]

Illustrations: No illustration located for this taxon.

Notes: This *Hypnum* has recently been documented in the Sweetwater Range just across the state line in Nevada. It is to be expected on rock walls (esp. volcanics) within the pinyon pine-Utah juniper woodlands in Mono Co.

Selected specimens: NEVADA: Douglas Co.: Desert Creek Canyon about 0.5 mile from Desert Creek Campground, Sweetwater Range, Toiyabe National Forest, *Shevock* 22167 (determined by Schofield).

***Racomitrium rysardii* Bednarek-Ochyra**
[Grimmiaceae]

Literature: Misapplied as *Racomitrium aquaticum* Christy and Wagner 1996. See Bednarek-Ochyra 2000.

Illustrations: Bednarek-Ochyra 2000. Misapplied as *Racomitrium aquaticum* Lawton 1971; Wagner 1998.

Notes: Although this species is currently not documented for California, *Racomitrium rysardii* should be looked for in the headwaters of the Applegate and Rogue River watersheds in California.

Selected specimens: OREGON: Multnomah Co.: Cascade Range west of Mt. Hood, *Rambo s.n.* (UC) [determined by Bednarek-Ochyra].

***Schistostega pennata* (Hedwig) Weber & D. Mohr** [Schistostegiaceae]

Illustrations: Lawton 1971.

Notes: Although this species is currently not recorded for California, a population approximately 35 air miles north of the California/Oregon state line appears to be the southernmost occurrence. Since suitable habitat for this species occurs in extreme northwest California, this species should eventually be located in the state.

Selected specimens: OREGON: Douglas Co.: Highway 138, south shore Diamond Lake, Umpqua National Forest, *Harpel 17848 & 18132* (CAS).

***Tayloria serrata* (Hedwig) Bruch & W. P. Schimper** [Splachnaceae]

Literature: Christy and Wagner 1996; Koch 1950a (based on Sayre 1935).

Illustrations: Crum and Anderson 1981; Ignatov and Ignatova 2003; Ireland 1982; Lawton 1971.

Notes: Christy and Wagner (1996) reference California within the species range. A population about 35 air miles north of the California/Oregon state line appears to be the southernmost record. This species is highly probable to occur in California.

Selected specimens: OREGON: Jackson Co.: Blue Lake Basin, Sky Lakes Wilderness, Rogue River National Forest, *Norris 52452*.

***Tomentypnum nitens* (Hedwig) Loeske** [Campyliaceae]

Literature: Koch 1950a; Spjut 1971. As *Campothecium nitens* Wynne 1943.

Illustrations: Flowers 1973.

Notes: Although habitat occurs for this moss in California, published reports for this moss in northern California are based on mis-identified material. We were unable to locate and confirm a Californian collection of this taxon. This species is documented for Oregon (Christy and Wagner 1999). *Tomentypnum nitens* should be searched for in meadow-fen areas with marble-limestone bedrock in the Klamath Mountains. A recent population was obtained by Jessup a few miles north of the state line.

Selected specimens: OREGON: Klamath Co.: off of Clover Creek about 4 km southeast of junction with Dead Indian Memorial Road, Buck Lake area, *Jessup 971004.14* (UC).

tive circumscriptions not selected in the current catalogue are also provided.

Acaulon muticum (Hedwig) Müller Hal. = *A. rufescens*
Acaulon muticum (Hedwig) Müller Hal. var. *rufescens* (A. Jaeger) Crum = *A. rufescens*

Acaulon rubrum Grout = *A. rufescens*

Acrocladium cuspidatum (Hedwig) Lindberg = *Calliergonella cuspidata*

Aloina aloides (Schultz) Kindberg = *A. ambigua*

Aloina aloides (Schultz) Kindberg var. *ambigua* (Bruch & Schimper) Craig in Grout = *A. ambigua*

Aloina pilifera (De Notaris) Crum & Anderson = *A. bifrons*

Aloina rigida var. *pilifera* (Bruch & Schimper) Limpricht = *A. bifrons*

Alsia abietina Sullivant = *Dendroalsia abietina*

Alsia californica var. *flagellifera* (Renauld & Cardot) Sullivant = *A. californica*

Alsia circinalis Sullivant & Kingman = *Dendroalsia abietina*

Alsia longipes Sullivant & Lesquereux = *Bestia longipes*

Amblystegiella jungermannioides (Bridel) Giacomini = *Platydictya jungermannioides*

Amblystegium americanum Grout = *Conardia compacta*

Amblystegium compactum (Müller Hal.) Austin = *Conardia compacta*

Amblystegium irriguum (Hooker & Wilson) Schimper in Bruch & Schimper = *Hygroamblystegium tenax*

Amblystegium riparium (Hedwig) Bruch & Schimper = *Leptodictyum riparium*

Amblystegium riparium var. *trichopodium* (Schultz) Bruch & Schimper = *Leptodictyum humile*

Amblystegium tenax (Hedwig) C. Jensen = *Hygroamblystegium tenax*

Ambystegium trichopodium (Schultz) Hartman = *Leptodictyum humile*

Amphoridium californicum Lesquereux & James = *Amphidium californicum*

Anacolia aristifolia Flowers in Grout = *A. menziesii*

Anacolia menziesii var. *baueri* (Hampe) Flowers in Grout = *A. baueri*

Anisothecium varium (Hedwig) Mitten (misapplied for California). See *Dicranella howei*

Anoetangium californicum Howe = *Amphidium californicum*

Anoetangium obtusifolium (Brotherus & Paris) Grout = *Molendoo sendmeriana*

Anomobryum filiforme (Dickson) Solms-Laubach in Rabenhorst = *A. julaceum*

Anomodon californicum Lesquereux = *Triquetrella californica*

Antitrichia californica var. *ambigua* Renauld & Cardot = *A. californica*

Antitrichia curtispindula (Hedwig) Bridel (in California) = *A. gigantea*

Antitrichia curtispindula var. *gigantea* Sullivant & Lesquereux = *A. gigantea*

Arctoa blyttii (Bruch & Schimper) Grout = *Kiaeria blyttii*

Arctoa falcata (Hedwig) Grout = *Kiaeria falcata*

Arctoa starkei (Weber & Mohr) Grout = *Kiaeria starkei*

Atractylocarpus stenocarpus (Wilson) Zander = *Campylopodidiella stenocarpa*

Atrichum oerstedianum (Müller Hal.) Mitten (in California) = *A. undulatum*

Atrichum undulatum var. *selwynii* (Austin) Grout = *A. selwynii*
Barbula acuta (Bridel) Bridel = *Didymodon rigidulus*

APPENDIX IV

SYNONYMS AND EXCLUDED NAMES

The history and application of scientific names applied to California mosses can be traced in part back to Hampe (1860), Sullivant (1864), Lesquereux (1868), Watson (1880) and Lesquereux and James (1884). This appendix lists the former names that have been used in the botanical literature for mosses attributed from California. Alterna-

- Barbula amplexa* Lesquereux = *Syntrichia amplexa*
Barbula arctocarpa Lesquereux = *Didymodon vinealis*
Barbula atrovirens Schimper = *Tortula atrovirens*
Barbula bakeri Cardot & Thériot = *Didymodon vinealis*
Barbula bolanderi Lesquereux = *Syntrichia bolanderi*
Barbula brachyphylla Sullivant = *Didymodon brachyphyllus*
Barbula brevipes Lesquereux = *Tortula brevipes*
Barbula chloronotos (Bridel) Bridel = *Crossidium squamiferum*
Barbula cylindrica (Taylor) Schimper = *Didymodon insulanus*
Barbula fallax Hedwig = *Didymodon fallax*
Barbula flexifolia Hampe = *Didymodon insulanus*
Barbula guelpinii Schimper = *Tortula guelpinii*
Barbula inermis Müller Hal. = *Tortula inermis*
Barbula insulana De Notaris = *Didymodon insulanus*
Barbula laevipila Bridel = *Syntrichia laevipila*
Barbula latifolia (Bruch ex Hartman) Hübener = *Syntrichia latifolia*
Barbula macrotricha Cardot & Thériot = *Tortula brevipes*
Barbula muelleri Bruch & Schimper = *Syntrichia princeps*
Barbula platyneura Müller Hal. & Kindberg = *Pseudocrossidium revolutum*
Barbula rigidula Schimper = *Didymodon rigidulus*
Barbula rubiginosa Mitten = *Didymodon occidentalis*
Barbula ruralis Hedwig = *Syntrichia ruralis*
Barbula semitorta Sullivant = *Didymodon vinealis*
Barbula subfallax Müller Hal. = *Didymodon insulanus*
Barbula subulata (Hedwig) P. Beauvois = *Tortula subulata*
Barbula vinealis Bridel = *Didymodon vinealis*
Barbula virescens Lesquereux = *Didymodon insulanus*
Bartramia fontana Hedwig = *Philonotis fontana*
Bartramia glauco-viridis Müller Hal. & Kindberg = *B. pomiformis*
Bartramia menziesii Turner = *Anacolia menziesii*
Bestia breweriana (Lesquereux) Grout = *Isothecium cristatum*
Bestia breweriana var. *howei* (Kindberg) Grout = *Isothecium cristatum*
Bestia breweriana var. *lutescens* Lesquereux & James = *Isothecium cristatum*
Bestia cristata (Hampe) L. Koch = *Isothecium cristatum*
Bestia holzingeri (Renauld & Cardot) Brotherus = *Bryolawtonia vancouveriensis*
Bestia occidentalis (Sullivant & Lesquereux) Grout = *Bryolawtonia vancouveriensis*
Bestia vancouveriensis (Kindberg) Wijk & Margadant = *Bryolawtonia vancouveriensis*
Blindia acuta var. *flexipes* Renauld & Cardot = *B. acuta*
Blindia flexipes (Renauld & Cardot) Kindberg = *B. acuta*
Brachythecium albicans var. *occidentale* Renauld & Cardot = *B. albicans*
Brachythecium bestii Grout = *B. reflexum*
Brachythecium californicum (Lesquereux) Jaeger = *Scleropodium californicum*
Brachythecium collinum var. *idahense* Renauld & Cardot = *B. velutinum*
Brachythecium curtum (Lindberg) Limpricht = *B. oedipodium*
Brachythecium erythrorrhizon var. *suberythrorrhizon* (Renauld & Cardot) Grout = *B. venustum*
Brachythecium lamprochryseum Müller Hal. & Kindberg = *B. frigidum*
Brachythecium latifolium Kindberg = *B. nelsoni*
Brachythecium pacificum Jennings = *B. asperrium*
Brachythecium petrophilum Williams = *B. venustum*
Brachythecium starkei (Bridel) Bruch & Schimper var. *explanatum* (Bridel) Mönkemeyer = *B. rutabulum*
Brachythecium subasperrium Cardot & Thériot = *B. frigidum*
Brachythecium suberythrorrhizon Renauld & Cardot = *B. venustum*
Brachythecium velutinum var. *venustum* (De Notaris) Arceangeli = *B. venustum*
Brachythecium washingtonianum Eaton in Grout = *B. asperrium*
Braunia californica Sullivant = *Pseudobraunia californica*
Bryum albicans (Wahlenberg) Roehling = *Pohlia wahlenbergii*
Bryum angustirete Kindberg = *B. algovicum*
Bryum argenteum var. *lanatum* (P. Beauvois) Hampe = *B. lanatum*
Bryum atwateriae Müller Hal. = *B. miniatum*
Bryum bigelovii Sullivant = *Pohlia ludwigii*
Bryum bolanderi Lesquereux = *Pohlia bolanderi*
Bryum californicum Sullivant = *B. bicolor*
Bryum ceruum (Hedwig) Bruch & Schimper = *B. uliginosum*
Bryum cirrhatum Hoppe & Hornschuch = *Bryum lisae*
Bryum commutatum Watson = *Pohlia drummondii*
Bryum crassirameum Renauld & Cardot = *B. pseudotriquetrum*
Bryum creberrimum Taylor = *B. lisae*
Bryum crudum Schreber = *Pohlia cruda*
Bryum cuspidatum (Bruch & Schimper) Schimper = *B. lisae*
Bryum dichotomum Hedwig = *B. bicolor*
Bryum duvallii Voit = *B. weigeli*
Bryum firmum Schreber = *B. pseudotriquetrum*
Bryum flagellosum Kindberg = *B. pseudotriquetrum*
Bryum hendersonii Renauld & Cardot = *B. canariense*
Bryum inclinatum (Bridel) Sturm = *B. amblyodon*
Bryum intermedium Bridel (misapplied for California). See *B. lisae*
Bryum lisae var. *cuspidatum* (Bruch & Schimper) Margadant = *B. lisae*
Bryum lonchocaulon Müller Hal. = *B. lisae*
Bryum microerythrocarpum Müller Hal. & Kindberg = *B. subapiculatum*
Bryum nudicaule Lesquereux = *Pohlia drummondii*
Bryum nutans var. *bicolor* (Hoppe & Hornschuch) Bruch & Schimper = *Pohlia nutans*
Bryum obconicum Hornschuch = *B. capillare*
Bryum occidentale Sullivant & Lesquereux = *B. capillare*
Bryum pendulum (Hornschuch) Schimper = *B. algovicum*
Bryum polymorphum Bruch & Schimper = *Pohlia elongata*
Bryum provinciale Philibert = *B. canariense*
Bryum pseudotriquetrum var. *bimum* (Bridel) Liljeblad = *B. bimum*
Bryum pseudotriquetrum var. *crassirameum* (Renauld & Cardot) Lawton = *B. pseudotriquetrum*
Bryum pyriforme Hedwig = *Leptobryum pyriforme*
Bryum sandbergii Holzinger = *Roellia roellii*
Bryum sanguilentum Renauld & Cardot = *B. capillare*
Bryum stenotrichum Müller Hal. = *B. amblyodon*
Bryum subdrepanocladum Cardot & Thériot = *B. capillare*
Bryum subrotundum Bridel = *B. pallescens*
Bryum tortifolium Funck in Bridel = *B. cyclophyllum*
Bryum tozeri Greville = *Epipterygium tozeri*

- Buxbaumia indusiata* Bridel = *B. viridis*
Calliargon stramineum (Bridel) Kindberg = *Straminergon stramineum*
Camptothecium aeneum (Mitten) Jaeger = *Homalothecium aeneum*
Camptothecium aeneum var. *dolosum* (Renauld & Cardot) Grout = *Homalothecium aeneum*
Camptothecium alsiioides Kindberg = *Homalothecium arenarium*
Camptothecium amesiae Renauld & Cardot = *Homalothecium pinnatifidum*
Camptothecium arenarium (Lesquereux) Jaeger = *Homalothecium arenarium*
Camptothecium dolosum Renauld & Cardot = *Homalothecium aeneum*
Camptothecium lutescens (Hedwig) Schimper in Bruch & Schimper (in California) = *Homalothecium fulgescens*
Camptothecium lutescens var. *fulgescens* (Mitten ex Müller Hal.) Persson = *Homalothecium fulgescens*
Camptothecium lutescens var. *occidentale* Renauld & Cardot = *Homalothecium fulgescens*
Camptothecium megaptitum Sullivant = *Trachybryum megaptitum*
Camptothecium nevadense Lesquereux = *Homalothecium nevadense*
Camptothecium nitens (Hedwig) Schimper = *Tomentypnum nitens*
Camptothecium nuttallii (Wilson) Schimper in Bruch & Schimper = *Homalothecium nuttallii*
Camptothecium nuttallii var. *stoloniferum* Lesquereux = *Homalothecium nuttallii*
Camptothecium pinnatifidum (Sullivant & Lesquereux) Sullivant = *Homalothecium pinnatifidum*
Campyliadelphus chrysophyllus (Bridel) Hedenäs = *Campylium chrysophyllum*
Campyliadelphus polygamus (Schimper in Bruch & Schimper) Kanda = *Campylium polygamum*
Campyliadelphus stellatus (Hedwig) Kanda = *Campylium stellatum*
Campylium polygamum var. *fluitans* Grout = *C. polygamum*
Campylopus atrovirens De Notaris (misapplied for California). See *C. schmidii*
Campylopus aureus Boscherelle & La Coste = *C. schmidii*
Catharinea callibryon Ehrhart = *Atrichum undulatum*
Catharinea undulata (Hedwig) Weber & Mohr = *Atrichum undulatum*
Ceratodon purpureus var. *conicus* (Hampe) Husnot = *C. purpureus*
Ceratodon purpureus var. *xanthopus* Sullivant = *C. purpureus*
Chenia leptophylla (Müller Hal.) Zander = *Leptophascum leptophyllum*
Chenia rhizophylla (Sakai) Zander = *Leptophascum leptophyllum*
Claopodium leuconeuron Sullivant & Lesquereux = *C. whippleanum*
Claopodium whippleanum var. *leuconeuron* (Sullivant & Lesquereux) Grout = *C. whippleanum*
Cratoneuron commutatum (Bridel) Roth = *Palustriella commutata*
Crossidium desertorum Holzinger & Bartram = *C. crassinerve*
Crossidium erosum Holzinger & Bartram = *C. crassinerve*
Crossidium griseum (Juratzka) Juratzka = *C. squamiferum*
Crossidium spatulaefolium Holzinger & Bartram = *C. aberrans*
Crossidium squamiferum var. *pottioideum* (De Notaris) Mönkemeyer = *C. squamiferum*
Desmatodon avenaceus Kingman = *Tortula obtusifolia*
Desmatodon californicus Lesquereux = *Tortula atrovirens*
Desmatodon convolutus (Bridel) Grout = *Tortula atrovirens*
Desmatodon glacialis Funck ex Bridel = *Tortula glacialis*
Desmatodon guepinii Bruch & Schimper = *Tortula guepinii*
Desmatodon heimii (Hedwig) Mitten = *Hennediella heimii*
Desmatodon hendersonii (Renauld & Cardot) Grout = *Didymodon tophaceus*
Desmatodon latifolius (Hedwig) Bridel = *Tortula euryphylla*
Desmatodon latifolius var. *muticus* (Bridel) Bridel = *Tortula glacialis*
Desmatodon leucostoma (R. Brown) Berggren = *Tortula leucostoma*
Desmatodon nervosus Kingman = *Tortula atrovirens*
Desmatodon nervosus var. *edentulus* Bruch & Schimper = *Tortula atrovirens*
Desmatodon obtusifolius (Schwägrichen) Schimper = *Tortula obtusifolia*
Desmatodon plinthobius Sullivant & Lesquereux = *Tortula plinthobia*
Desmatodon sprengelii (Schwägrichen) Williams = *Plaubelia sprengelii*
Desmatodon stomatodontus (Cardot) Williams = *Plaubelia sprengelii*
Desmatodon suberectus (Hooker) Limpricht = *Tortula leucostoma*
Desmatodon systylius Schimper = *Tortula systylia*
Dichelyma falcatum (Hedwig) Myrin var. *uncinatum* (Mitten) Lawton = *D. uncinatum*
Dichelyma swartzii Lesquereux = *Warnstorfia fluitans*
Dichodontium pellucidum var. *fagimontanum* (Bridel) Kindberg = *D. pellucidum*
Dicranella rubra Lindberg (misapplied for California). See *D. howei*
Dicranella varia (Hedwig) Schimper (misapplied for California). See *D. howei*
Dicranoweisia crispula (Hedwig) Milde (misapplied for California). See *D. contermina*
Dicranoweisia crispula (Hedwig) Milde var. *contermina* (Renauld & Cardot) Grout = *D. contermina*
Dicranum heteromallum Hedwig = *Dicranella heteromallum*
Dicranum palustre Bachelot de la Pylaie = *Dicranella howei*
Dicranum strictum Schleicher ex Mohr (misapplied for California). See *Orthodicranum tauricum*
Dicranum subulatum Hedwig = *Dicranella subulata*
Dicranum tauricum Sapehin = *Orthodicranum tauricum*
Dicranum varium Hedwig (misapplied for California). See *Dicranella howei*
Dicranum virens var. *compactum* Bruch & Schimper = *Oncophorus virens*
Dicranum virens var. *serratum* Bruch & Schimper = *Oncophorus virens*
Didymodon acutus (Bridel) Saito = *D. rigidulus*
Didymodon australasiae var. *umbrosus* (Müller Hal.) Zander = *D. umbrosus*
Didymodon columbianus Hermann & Lawton = *Bryoerythrophyllum columbianum*

- Didymodon mexicanus* Beschereille = *D. rigidulus*
Didymodon mexicanus var. *subulatus* Thériot & Bartram = *D. rigidulus*
Didymodon recurvirostris (Hedwig) Jennings = *Bryoerythrophyllum recurvirostrum*
Didymodon rigidulus var. *icmadophila* (Schimper ex Müller Hal.) Zander = *D. rigidulus*
Didymodon rigidulus var. *subulatus* (Thériot & Bartram) Zander = *D. rigidulus*
Didymodon rubellus Bruch & Schimper = *Bryoerythrophyllum recurvirostrum*
Didymodon trifarius (Hedwig) Bridel = *D. luridus*
Didymodon vinealis var. *brachyphyllus* (Sullivant in Whipple) Zander = *D. brachyphyllus*
Didymodon vinealis var. *flaccidus* (Bruch & Schimper) Zander = *D. insulanus*
Didymodon vinealis var. *luridus* Hornschuch = *D. luridus*
Didymodon vinealis var. *nicholsonii* (Culmann) Zander = *D. nicholsonii*
Didymodon vinealis var. *rubiginosus* (Müller Hal.) Zander = *D. occidentalis*
Ditrichum cylindricus (Hedwig) Grout = *Trichodon cylindricus*
Drepanocladus aduncus var. *knieffii* (Bruch & Schimper) Mönkemeyer = *D. aduncus*
Drepanocladus aduncus var. *polycarpus* (Blandow) Warnstorf forma *capillifolius* (Warnstorf) Mönkemeyer = *D. capillifolius*
Drepanocladus exannulatus (Bruch & Schimper) Warnstorf = *Warnstorfia exannulata*
Drepanocladus fluitans (Hedwig) Warnstorf = *Warnstorfia fluitans*
Drepanocladus polygamus (Bruch & Schimper) Hedenäs = *Campyllum polygamum*
Drepanocladus sendtneri (Schimper ex Müller Hal.) Warnstorf (in California) = *D. sordidus*
Drepanocladus uncinatus (Hedwig) Warnstorf = *Sanionia uncinata*
Drepanocladus vernicosus (Mitten) Warnstorf = *Hamatacaulis vernicosus*
Dryptodon patens (Hedwig) Bridel = *Grimmia ramondii*
Encalypta vulgaris var. *muticus* Bridel = *E. vulgaris*
Encalypta vulgaris var. *rhaptocharpa* (Schwägrichen) Lawton = *E. rhaptocharpa*
Entosthodon muelenbergii (Turner) Fife = *Funaria muelenbergii*
Entosthodon templetoni Schwägrichen = *E. attenuatus*
Ephemerum serratum var. *angustifolium* Bruch & Schimper = *E. serratum*
Ephemerum serratum var. *minutissimum* (Lindberg) Grout = *E. serratum*
Eurhynchium brittoniae Grout = *Kindbergia oregana*
Eurhynchium colpophyllum Sullivant = *Scleropodium colpophyllum*
Eurhynchium diversifolium Schimper in Bruch & Schimper = *E. pulchellum*
Eurhynchium oreganum (Sullivant) Jaeger = *Kindbergia oregana*
Eurhynchium praelongum (Hedwig) Bruch & Schimper = *Kindbergia praelonga*
Eurhynchium praelongum var. *californicum* Grout = *Kindbergia praelonga*
Eurhynchium praelongum var. *stokesii* (Turner) Dixon = *Kindbergia praelonga*
Eurhynchium pulchellum var. *barnesii* (Renauld & Cardot) Crum, Steere, & Anderson = *E. pulchellum*
Eurhynchium riparioides (Hedwig) P. Richards = *Platyhypnidium riparioides*
Eurhynchium rusciforme (Bridel) Milde = *Platyhypnidium riparioides*
Eurhynchium serratum (Hedwig) Kindberg = *Steerecleus serrulatus*
Eurhynchium stokesii (Turner) Schimper in Bruch & Schimper = *Kindbergia praelonga*
Eurhynchium strigosum (Weber & Mohr) Schimper = *E. pulchellum*
Eurhynchium substrigosum Kindberg in Macoun & Kindberg = *E. pulchellum*
Eurhynchium substrigosum var. *scabrisetum* Grout = *E. pulchellum*
Fabronia ciliaris ssp. *gymnostoma* (Sullivant & Lesquereux) Grout = *F. ciliaris*
Fabronia gymnostoma Sullivant & Lesquereux in Sullivant = *F. ciliaris*
Fabronia octoblepharis Schwägrichen = *F. ciliaris*
Fissidens cristatus Wilson ex Mitten = *F. dubius*
Fissidens julianus (Montagne) Schimper = *F. fontanus*
Fissidens limbatus Sullivant = *F. crispus*
Fissidens limbatus var. *ensiformis* Grout = *F. bryoides*
Fissidens milo-bakeri L. Koch = *F. curvatus*
Fissidens rufulus Bruch & Schimper (misapplied for California). See *F. ventricosus*
Fontinalis antipyretica var. *gigantea* Sullivant = *F. gigantea*
Fontinalis antipyretica var. *mollis* (Müller Hal.) Welch in Grout = *F. mollis*
Fontinalis antipyretica var. *oregonensis* Renauld & Cardot = *F. chrysophylla*
Fontinalis antipyretica var. *patula* (Cardot) Welch in Grout = *F. antipyretica*
Fontinalis californica Sullivant = *F. antipyretica*
Fontinalis duriae Schimper = *F. hypnoides*
Fontinalis hypnoides Hartman var. *duriae* (Schimper) Husnot = *F. duriae*
Fontinalis kindbergii (Lesquereux) Renauld & Cardot = *F. howellii*
Fontinalis mercediana Lesquereux = *F. neomexicana*
Fontinalis nitida Lindberg & Arnell = *F. hypnoides*
Fontinalis patula Cardot = *F. antipyretica*
Funaria bolanderi (Lesquereux) Holzinger in Brotherus = *Entosthodon bolanderi*
Funaria calcarea Wahlenberg = *F. muelenbergii*
Funaria californica Sullivant & Lesquereux = *Entosthodon californicus*
Funaria convoluta Hampe = *F. hygrometrica*
Funaria hibernica (Hooker) Boulay = *F. muelenbergii*
Funaria hygrometrica var. *convoluta* (Hampe) Grout = *F. hygrometrica*
Funaria hygrometrica var. *utahensis* Grout = *F. hygrometrica*
Funaria mediterranea Lindberg = *F. calcarea*
Funaria muelenbergii var. *lineata* Grout = *F. muelenbergii*
Funaria muelenbergii var. *patula* Bruch & Schimper = *F. muelenbergii*
Funaria rubriseta Bartram = *Entosthodon rubrisetum*
Funaria tusconi Bartram = *Entosthodon tusconi*
Grimmia ancistrodes Durieu de Maisonneuve in Montagne = *G. trichophylla*
Grimmia affinis Hornschuch = *G. longirostris*
Grimmia agassizii (Sullivant & Lesquereux) Lesquereux & James = *Schistidium agassizii*
Grimmia alpestris var. *manniae* Müller Hal. = *G. caespiticia*
Grimmia alpicola Hedwig = *Schistidium agassizii*
Grimmia alpicola var. *dupretii* (Thériot) Crum = *Schistidium dupretii*

- Grimmia alpicola* var. *rivularis* (Bridel) Brotherus = *Schistidium rivulare*
- Grimmia apocarpa* Hedwig (misapplied for California). See *Schistidium apocarpum* (Appendix II)
- Grimmia apocarpa* var. *ambigua* (Sullivant) Grout (misapplied for California). See *Schistidium apocarpum* (Appendix II)
- Grimmia apocarpa* var. *conferta* (Funck) Sprengel = *Schistidium confertum*
- Grimmia apocarpa* var. *gracilis* (Schleicher) Weber & Mohr (misapplied for California). See *Schistidium apocarpum* (Appendix II)
- Grimmia apocarpa* var. *pulvinata* (Hedwig) Grout = *Schistidium pulvinatum*
- Grimmia apocarpa* var. *tenerrima* Nees, Hornschuch, & Sturm (misapplied for California) See *Schistidium apocarpum* (Appendix II)
- Grimmia atricha* Müller Hal. & Kindberg = *Schistidium atrichum*
- Grimmia brevirostris* Williams = *G. hamulosa*
- Grimmia californica* Sullivant in Whipple = *G. lisae*
- Grimmia calyptrata* Hooker in Drummond = *Coscinodon calyptratus*
- Grimmia catalinensis* Barttram = *G. ovalis*
- Grimmia cinclidodontea* Müller Hal. in Röhl = *Schistidium cinclidodonteum*
- Grimmia commutata* Hübener = *G. ovalis*
- Grimmia conferta* Funck = *Schistidium confertum*
- Grimmia curvata* (Bridel) DeSloover = *G. ramondii*
- Grimmia decipiens* auct (misapplied for California). See *G. trichophylla*
- Grimmia dupretii* Thériot = *Schistidium dupretii*
- Grimmia flaccida* (De Notaris) Lindberg = *Schistidium flaccidum*
- Grimmia hartmanii* Schimper (misapplied for California). See *G. anomala*
- Grimmia hartmanii* var. *anomala* (Hampe) Mönkemeyer = *G. anomala*
- Grimmia heterophylla* Kindberg in Macoun = *Schistidium heterophyllum*
- Grimmia heterosticha* Howe = *Racomitrium heterostichum*
- Grimmia leucophaea* Greville = *G. laevigata*
- Grimmia maritima* Turner = *Schistidium maritimum*
- Grimmia muhlenbeckii* Schimper = *G. trichophylla*
- Grimmia nevii* Müller Hal. ex Mohr = *Racomitrium aciculare*
- Grimmia occidentalis* Lawton = *Schistidium occidentale*
- Grimmia pacifica* Lawton = *Schistidium cinclidodonteum*
- Grimmia raii* Austin = *Jaffuelobryum raii*
- Grimmia scouleri* Müller Hal. = *Scouleria aquatica*
- Grimmia sessitana* De Notaris (excluded for California). See *G. reflexidens*
- Grimmia tenera* Zetterstedt = *Schistidium tenerum*
- Grimmia tenerrima* Renauld & Cardot = *G. reflexidens*
- Grimmia trichophylla* var. *brachycarpa* De Notaris = *G. lisae*
- Grimmia trichophylla* var. *meridionalis* Müller Hal. = *G. trichophylla*
- Grimmia trichophylla* var. *muhlenbeckii* (Schimper) Husnot = *G. trichophylla*
- Grimmia watsoni* Lesquereux & James = *G. trichophylla*
- Grimmia wrightii* (Sullivant in Gray) Austin = *Jaffuelobryum wrightii*
- Gymnostomum aeruginosum* Small (misapplied for California). See *Gymnostomum calcareum*
- Gymnostomum calcareum* var. *perpusillum* Sullivant = *G. calcareum*
- Gymnostomum recurvirostre* Hedwig = *Hymenostylium recurvirostre*
- Harpidium exannulatum* (Schimper in Bruch & Schimper) C. E. O. Jensen = *Warnstorfia exannulata*
- Hedwigia albicans* Lindberg (misapplied for California). See *H. detonsa*, *H. stellata*
- Hedwigia albicans* var. *detonsa* Howe = *H. detonsa*
- Hedwigia ciliata* (Hedwig) P. Beauvois (misapplied for California). See *H. detonsa*, *H. stellata*
- Hedwigia ciliata* var. *detonsa* (Howe) Paris = *H. detonsa*
- Heterocladium aberrans* Renauld & Cardot = *H. procurrens*
- Heterocladium heteropteroides* Best = *H. macounii*
- Heterocladium heteropteroides* var. *filesceus* Best = *H. macounii*
- Heterophyllum haldanianum* (Greville) Kindberg = *Callicladium haldanianum*
- Homalothecium aureum* (Spruce) Robinson (misapplied for California). See *H. pinnatifidum*
- Homalothecium megaptilum* (Sullivant) H. Robinson = *Trachybryum megaptilum*
- Homalothecium nitens* (Hedwig) H. Robinson = *Tomentypnum nitens*
- Homalothecium nuttallii* var. *hamatidens* Kindberg = *H. nuttallii*
- Homalothecium nuttallii* var. *tenue* Kindberg = *H. nuttallii*
- Husnotiella palmeri* Cardot = *Didymodon revolutus*
- Husnotiella pringlei* Cardot = *Didymodon tophaceus*
- Husnotiella revoluta* Cardot = *Didymodon revolutus*
- Husnotiella revoluta* var. *palmeri* (Cardot) Thériot = *Didymodon revolutus*
- Hydrogrimmia mollis* (Bruch & Schimper) Loeske = *Grimmia mollis*
- Hygroamblystegium irriguum* (Hooker & Wilson) Loeske = *H. tenax*
- Hygrohypnum dilatatum* (Wilson) Loeske = *H. duriusculum*
- Hygrohypnum palustre* Loeske = *H. luridum*
- Hygrohypnum smithii* var. *gouldarii* (Schimper) Wijk & Margadant = *H. cochlearifolium*
- Hymenostomum inoperculatum* Crum = *Weissia inoperculata*
- Hymenostomum tortile* (Schwägrichen) Bruch & Schimper = *Weissia condensa*
- Hyophila stanfordensis* (Steere) Smith & Whitehouse = *Hennediella stanfordensis*
- Hypnum aduncum* Hedwig = *Drepanocladus aduncus*
- Hypnum aggregatum* Mitten = *Isothecium cristatum*
- Hypnum arcticum* Sommerfelt in Wahlenberg = *Hygrohypnum smithii*
- Hypnum arenarium* Lesquereux = *Homalothecium arenarium*
- Hypnum asperillum* Mitten ex Müller Hal. = *Brachythecium asperillum*
- Hypnum bestii* (Renauld & Bryhn) Renauld & Bryhn = *Hygrohypnum bestii*
- Hypnum bigelovii* Sullivant = *Porotrichum bigelovii*
- Hypnum brewerianum* Lesquereux = *Isothecium cristatum*
- Hypnum caespitosum* Wilson = *Scleropodium cespitosum*
- Hypnum californicum* Lesquereux = *Scleropodium californicum*
- Hypnum collinum* Schleicher ex Müller Hal. = *Brachythecium collinum*
- Hypnum colpophyllum* Sullivant = *Scleropodium colpophyllum*
- Hypnum commutatum* Hedwig = *Palustriella commutata*

- Hypnum crispifolium* Hooker = *Claopodium crispifolium*
Hypnum denticulatum Hedwig = *Plagiothecium denticulatum*
Hypnum exannulatum var. *cochleae* Austin = *Warnstorfia exannulata*
Hypnum hillebrandi Lesquereux = *Brachythecium collinum*
Hypnum illecebrum Schwägrichen = *Scleropodium tour-etii*
Hypnum lutescens Hedwig = *Homalothecium fulgescens*
Hypnum myosuroides Hedwig = *Isothecium myosuroides*
Hypnum nevadense Lesquereux = *Homalothecium nevadense*
Hypnum nuttallii Wilson = *Homalothecium nuttallii*
Hypnum ochraceum Turner ex Wilson = *Hygrohypnum ochraceum*
Hypnum oregonum Sullivant = *Kindbergia oregana*
Hypnum pinnatifidum Sullivant = *Homalothecium pinnatifidum*
Hypnum populeum Hedwig = *Brachythecium populeum*
Hypnum praelongum Hedwig = *Kindbergia praelonga*
Hypnum pseudo-arcticum Kindberg = *Hygrohypnum luridum*
Hypnum riparium Hedwig = *Leptodictyum riparium*
Hypnum rusciforme Hedwig = *Platyhypnidium riparioides*
Hypnum sendtneri Müller Hal. (misapplied for California). See *Drepanocladus sordidus*
Hypnum serpens Hedwig = *Amblystegium serpens*
Hypnum strigosum Hedwig = *Eurhynchium pulchellum*
Hypnum uncinatum Hedwig = *Sanionia uncinata*
Hypnum undulatum Hedwig = *Buckiella undulata*
Hypnum vallum Lesquereux = *Brachythecium asperrium*
Hypnum whippleanum Sullivant = *Claopodium whippleanum*
Isopterygium borrierianum (Müller Hal.) Lindberg = *Pseudotaxiphyllum elegans*
Isopterygium elegans (Bridel) Lindberg = *Pseudotaxiphyllum elegans*
Isopterygium pulchellum (Hedwig) Jaeger = *Isopterygiopsis pulchella*
Isopterygium seligeri (Bridel) Dixon in C. Jensen = *Herzogiella seligeri*
Isothecium brewerianum (Lesquereux) Kindberg in Macoun = *I. cristatum*
Isothecium howei Kindberg = *I. cristatum*
Kindbergia brittoniae (Grout) Ochyra = *K. oregana*
Kindbergia praelonga var. *stokesii* (Turner) Ochyra = *K. praelonga*
Leersia rhapsocarpa (Schwägrichen) Lindberg = *Encalypta rhapsocarpa*
Leersia trachymitria (Ripart) Holzinger in Coville = *Encalypta rhapsocarpa*
Leptodictyum trichopodium (Schultz) Warnstorf = *L. humile*
Leptodon circinnatus Sullivant = *Dendroalsia abietina*
Leptotrichum schimperi Lesquereux = *Ditrichum schimperi*
Lescuraea incurvata var. *gigantea* Lawton = *L. incurvata*
Lescuraea incurvata var. *tenuiretis* (Culmann) Lawton = *L. incurvata*
Lescuraea radicata var. *compacta* (Best) Lawton = *L. radicata*
Lescuraea radicata var. *denudata* (Kindberg) Lawton = *L. radicata*
Lescuraea radicata var. *pallida* (Best) Lawton = *L. pallida*
Leskeella tectorum (Bridel ex Hagen) = *Pseudoleskeella tectorum*
Leucolepis menziesii (Hooker) Steere ex L. Koch = *L. acanthoneura*
Limnobia bestii (Renauld & Bryhn) Holzinger = *Hygrohypnum bestii*
Limnobia palustre Bruch & Schimper = *Hygrohypnum luridum*
Merceya latifolia Kindberg = *Crumia latifolia*
Mielichhoferia mielichhoferiana (Funck in Hooker) Loeske (misapplied for California). See *M. elongata*
Mildeella bryoides Howe = *Tortula protobryoides*
Mniobryum albicans (Wahlenberg) Limpricht = *Pohlia wahlenbergii*
Mniobryum longibracteatum (Brotherus in Röhl) Brotherus = *Pohlia longibracteata*
Mniobryum wahlenbergii (Weber & Mohr) Jennings = *Pohlia wahlenbergii*
Mnium affine Blandow ex Funck (misapplied for California). See *Plagiomnium ellipticum*
Mnium affine var. *rugicum* (Laurer) Bruch & Schimper = *P. rugicum*
Mnium cuspidatum Hedwig = *Plagiomnium cuspidatum*
Mnium glabrescens Kindberg = *Rhizomnium glabrescens*
Mnium insigne Mitten = *Plagiomnium insigne*
Mnium longirostrum Bridel = *Plagiomnium rostratum*
Mnium lycopodioides Schwägrichen (in North America) = *Mnium ambiguum*
Mnium medium Bruch & Schimper = *Plagiomnium medium*
Mnium menziesii (Hooker) Müller Hal. = *Leucolepis acanthoneura*
Mnium nudum Williams = *Rhizomnium nudum*
Mnium orthorrhynchum auct. plur. = *M. thomsonii*
Mnium perssonii T. Koponen = *Rhizomnium magnifolium*
Mnium pseudopunctatum Bruch & Schimper = *Rhizomnium pseudopunctatum*
Mnium punctatum Hedwig = *Rhizomnium punctatum*
Mnium punctatum var. *elatum* Schimper = *Rhizomnium magnifolium*
Mnium rostratum Schrader = *Plagiomnium rostratum*
Mnium rugicum Laurer = *P. ellipticum*
Mnium venustum Mitten = *Plagiomnium venustum*
Neckera menziesii Hooker in Drummond = *Metaneckera menziesii*
Neckeradelphus menziesii (Hooker) Steere = *Metaneckera menziesii*
Octodicerus fontanus (Bachelot de la Pylaie) Lindberg = *Fissidens fontanus*
Octodicerus julianum (A. P. de Candolle) Bridel = *Fissidens fontanus*
Oligotrichum lyellii (Mitten) Lindberg = *Meiotrichum lyallii*
Oncophorus jenneri (Schimper) Williams = *Cynodontium jenneri*
Orthotheciella varia (Hedwig) Ochyra = *Amblystegium varium*
Orthotrichum coulteri Lesquereux = *O. tenellum*
Orthotrichum cupulatum var. *jamesianum* (Sullivant in Watson) Lawton = *O. pellucidum*
Orthotrichum cylindrocarpum Lesquereux in Jaeger = *O. tenellum*
Orthotrichum epapillosum Lawton & Hermann = *O. eurphyllum*
Orthotrichum jamesianum Sullivant ex James in Watson = *O. pellucidum*
Orthotrichum kingianum Lesquereux = *O. laevigatum*

- Orthotrichum laevigatum* var. *kingianum* (Lesquereux) Grout = *O. laevigatum*
Orthotrichum laevigatum forma *macounii* (Austin) Lawton & Vitt = *O. laevigatum*
Orthotrichum lyellii var. *howei* Renauld & Cardot = *O. lyellii*
Orthotrichum lyellii var. *papillosum* (Hampe) Sullivant = *O. papillosum*
Orthotrichum microblepharum Schimper = *O. pylaisii*
Orthotrichum roellii Venturi in Röhl = *O. laevigatum*
Orthotrichum rupestre var. *globosum* (Lesquereux) Grout = *O. rupestre*
Orthotrichum sturmii Hoppe & Hornschuch = *O. rupestre*
Orthotrichum tenellum var. *coulteri* Lesquereux = *O. tenellum*
Orthotrichum texanum var. *globosum* Lesquereux = *O. texanum*
Palustriella falcata (Bridel) Hedenäs (for California) = *P. commutata*
Phascum cuspidatum var. *americanum* Renauld & Cardot = *P. cuspidatum*
Phascum hyalinotrichum Cardot & Thériot = *Stegonia hyalinotricha*
Philonotis fontana var. *americana* (Dismier) Flowers = *P. americana*
Philonotis fontana var. *caespitosa* (Juratzka) Schimper = *P. caespitosa*
Philonotis fontana var. *pumila* Bridel = *P. tomentella*
Physcomitrella californica Crum & Anderson = *P. readeri*
Physcomitrella patens var. *californica* (Crum & Anderson) Tan = *P. readeri*
Physcomitrella patens ssp. *readeri* (Müller Hal.) Tan = *P. readeri*
Physcomitrium megalocarpum Kindberg = *P. pyriforme*
Physcomitrium megalocarpum var. *californicum* (Britton) Grout = *P. californicum*
Physcomitrium turbinatum (Michaux) Britton = *P. pyriforme*
Plagiommium rugicum (Laurer) T. Koponen = *P. ellipticum*
Plagiothecium elegans (Hooker) Sullivant = *Pseudotaxiphyllum elegans*
Plagiothecium pulchellum (Hedwig) Bruch & Schimper = *Isopterygiopsis pulchella*
Plagiothecium roeseanum Bruch & Schimper = *P. cavifolium*
Plagiothecium seligeri (Bridel) Lindberg = *Herzogiella seligeri*
Plagiothecium striatellum (Bridel) Lindberg = *Herzogiella striatella*
Plagiothecium sylvaticum (Bridel) Bruch & Schimper = *P. denticulatum*
Plagiothecium sylvaticum var. *roeseanum* (Bruch & Schimper) Lindberg = *P. cavifolium*
Plagiothecium undulatum (Hedwig) Schimper in Bruch & Schimper = *Buckiella undulata*
Plaubelia sprengelii var. *stomatodonta* (Cardot) Zander = *P. sprengelii*
Pleuridium alternifolium var. *howei* Renauld & Cardot = *P. subulatum*
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Pleuridium bakeri var. *elongatum* Cardot & Thériot = *P. acuminatum*
Pleuridium bolanderi Müller Hal. ex Jaeger = *P. acuminatum*
Pleuridium californicum Grout = *P. acuminatum*
Pleuridium stramineum Lesquereux ex Austin = *P. acuminatum*
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- Rhizomnium perssonii* T. Koponen = *R. magnifolium*
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- Scleropodium apocladum* (Mitten) Grout = *S. cespitans*
- Scleropodium caespitosum* (Wilson) Bruch & Schimper = *S. cespitans*
- Scleropodium caespitosum* var. *sublaeve* Renault & Cardot = *S. cespitans*
- Scleropodium cespitans* var. *sublaeve* (Renault & Cardot) Wijk & Margadant = *S. cespitans*
- Scleropodium illecebrum* Schimper in Bruch & Schimper = *S. touretii*
- Scleropodium touretii* var. *colpophyllum* (Sullivant) Lawton = *S. colpophyllum*
- Scopelophila latifolia* (Kindberg) Renault & Cardot = *Crumia latifolia*
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- Sphagnum auriculatum* Schimper (in California) = *S. lescurii*
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- Sphagnum cymbifolium* (Ehrhart) Hedwig = *S. palustre*
- Sphagnum plumulosum* Röhl = *S. subnitens*
- Sphagnum recurvum* var. *brevifolium* (Lindberg ex Braithwaite) Warnstorf = *S. fallax*
- Sphagnum recurvum* var. *tenue* Klinggräff = *S. angustifolium*
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- Sphagnum subsecundum* var. *rufescens* (Nees & Hornschuch) Hübener = *S. lescurii*
- Stableria gracilis* (Bruch & Schimper) Lindberg in Braithwaite = *Orthodontium gracile*
- Stableria gracilis* var. *californica* Howe = *Orthodontium gracile*
- Stokesiella oregana* (Sullivant) H. Robinson = *Kindbergia oregana*
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- Thamnium holzingeri* Renault & Cardot = *Bryolawtonia vancouveriensis*
- Thamnium leibergii* Britton = *Thamnobryum neckeroides*
- Thamnobryum leibergii* (Britton) Renault & Cardot = *T. neckeroides*
- Timmia megapolitana* Hedwig var. *bavarica* (Hessler) Bridel = *T. bavarica*
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- Timmia vancouveriensis* Brotherus in Röhl = *T. crassinervis*
- Tortella tortelloides* (S. W. Greene) Robinson (for California) = *T. alpicola*
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- Tortula angustata* Howe = *T. subulata*
- Tortula atherodes* Zander = *Phascum cuspidatum*
- Tortula aurea* Bartram = *Pseudocrossidium crinitum*
- Tortula bartramii* Steere in Grout = *Syntrichia bartramii*
- Tortula bistratosa* Flowers = *Syntrichia caninervis*
- Tortula bolanderi* (Lesquereux) Howe = *Syntrichia bolanderi*
- Tortula caninervis* (Mitten) Brotherus = *Syntrichia caninervis*
- Tortula desertorum* Brotherus = *Syntrichia caninervis*
- Tortula elata* (Müller Hal.) Durieu de Maisonnue = *Didymodon vinealis*
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- Tortula intermedia* (Bridel) De Notaris = *Syntrichia ruralis*

Tortula laevipila (Bridel) Schwägrichen = *Syntrichia laevipila*
Tortula laevipila var. *meridionalis* (Schimper) Wijk & Margadant = *Syntrichia laevipila* var. *meridionalis*
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Tortula pagorum (Milde) De Notaris = *Syntrichia pagorum*
Tortula papillosissima (Coppey) Brotherus = *Syntrichia papillosissima*
Tortula princeps De Notaris = *Syntrichia princeps*
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Trichostomopsis fayae Grout = *Didymodon australasiae*
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Trichostomum anomalum Bruch & Schimper = *Timmiella anomala*
Trichostomum cylindricum (Bruch) Müller Hal. = *Oxystegus tenuirostris*
Trichostomum flavo-virens var. *crassinerve* (Hampe) Lesquereux & James = *Timmiella crassinervis*
Trichostomum flexipes Bruch & Schimper = *Timmiella crassinervis*
Trichostomum rigidulum (Hedwig) Turner = *Didymodon rigidulus*
Trichostomum tenuirostre (Hooker & Taylor) Lindberg = *Oxystegus tenuirostris*
Trichostomum tophaceum Bridel = *Didymodon tophaceus*
Triquetrella papillata (Hooker f. & Wilson) Brotherus (in California) = *T. californica*
Ulotia crispa (Hedwig) Bridel (in California) = *Ulotia obtusiuscula*
Ulotia crispa (Hedwig) Bridel var. *alaskana* (Cardot & Thériot) Grout = *Ulotia crispa*
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Webera albicans Schimper = *Pohlia wahlenbergii*
Webera bolanderi (Lesquereux) Lesquereux & James = *Pohlia bolanderi*
Webera commutata Schimper = *Pohlia drummondii*
Webera cruda (Hewig) Fürnrohr = *Pohlia cruda*
Webera nudicaulis Lesquereux & James = *Pohlia drummondii*
Webera polymorpha (Hoppe & Hornschuch) Schimper = *Pohlia elongata*
Webera tozeri (Greville) Schimper = *Epipterygium tozeri*
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Weissia glauca Bartram = *W. andersoniana*
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Editor—DR. JOHN CALLAWAY
Dept. of Environmental Science
University of San Francisco
2130 Fulton Street
San Francisco, CA 94117-1080
callaway@usfca.edu

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CONTRIBUTIONS TOWARD A BRYOFLOTA OF CALIFORNIA: II. A KEY TO THE MOSSES

DANIEL H. NORRIS

University Herbarium, University of California, Berkeley, CA 94720-2465
dhnorris@uclink.berkeley.edu

JAMES R. SHEVOCK

Department of Botany, California Academy of Sciences,
San Francisco, CA 94118-4599

ABSTRACT

Keys are provided for the 731 species in 200 genera of mosses known from the states of Washington, Oregon, Nevada and California, as well as from Baja California Norte, Mexico. These keys emphasize differential characters of the gametophyte as primary distinguishing features.

Key Words: Mosses, California, Oregon, Washington, Nevada, Baja California Norte, identification keys.

These keys are intended to facilitate the identification of mosses in California but they should be useful throughout most of the states of the USA west of the Rocky Mountains. The key includes all mosses currently known from Washington, Oregon, California and from Baja California Norte.

It is our intent that these keys will be used in conjunction with the "Catalogue of California Mosses" (Norris and Shevock 2004). The catalogue provides a list of publications that contain detailed illustrations of nearly every California moss covered in these keys. Illustrations can provide a high level of confirmation once a species has been tentatively identified. In addition, the California moss catalogue provides a list of representative specimens that are chosen to reflect the geographic and ecological range of each species within the state. Close examination of the reported distribution will reveal whether a range extension is being documented. The California moss catalogue also contains a rather large listing of pertinent literature.

Use of these keys requires both a compound microscope and a dissection microscope. The compound microscope should have an optical micrometer capable of measuring cell size in micrometers. It should be noted here that previous bryophyte floras differ one to another in patterns of cell measurement. Are cell measurements simply a measurement of the width of the lumen; or are those measurements that of the lumen plus one of the walls? If the plant has thick walls, this difference in measurement technique may be highly consequential. The majority of works, including our present report, give the cell size to include both lumen and a lateral wall.

Use of these keys requires careful attention to the wording. Sometimes the generic or species keys refer to characters not uniformly present in all plants included in that section. The words "sometimes," "usually," "mostly," and "often" are placed in the key to provide for those instances.

Dissection of a moss requires the removal of individual leaves for mounting on a slide under a cover slip. Such dissection can be accomplished with a pair of straight dissection needles: one for holding the stem in place on the slide and one for scraping leaves from the stem. Mosses with easily fragmented leaves can be prepared by holding the leafy stem in place with a straight dissection needle and scraping with a sword-point needle or with a razor blade. Mosses with very decurrent leaves should be held in place with a needle with the leaves pulled from the stem with fine-point forceps.

Many mosses, especially the erect and unbranched (acrocarpous) genera require cross-sectioning of individual leaves. That can be accomplished with a straight dissection needle that is used to hold the leaf in place, and with a regularly replaced (therefore, new) single-edged razor-blade. A slight chopping motion by a razor blade across the supporting needle should cut a leaf at about its mid-line. Subsequent chops remove individual cross-sections that are so thin as to turn on their sides allowing full view of the cross-section under the compound microscope. With experience and practice each worker develops particular techniques found to be useful.

Nearly all mosses can be identified solely on the basis of examination of the leafy plant (the gametophyte). It is also useful, and occasionally necessary, to examine features of the spore-bearing axis (the sporophyte). Even under a dissection microscope, one can observe features of the capsule shape and orientation, as well as seta length and calyptra morphology. One does, however, need more dissection and magnification to examine the cellular morphology of the capsule wall epidermis (exothecial cells), and especially those of the teeth that line the capsule mouth (peristome teeth). Preparation of a capsule

for viewing requires a simple longitudinal razor-blade cut of the capsule with subsequent arrangement of the resulting identical halves of that capsule. Features of the exothecial cells require viewing under the compound scope of the outer surface of the median capsule wall. Features of the peristome are best viewed by orienting the two capsule halves so that each surface is exposed to view.

"Keys are effective ways to identify a plant when the person already knows the name of that plant or, at least knows what it is not." Keys never work perfectly and should here be used primarily to give one an idea of what is being examined. After keying a moss, a professional bryologist will ordinarily confirm it by comparing it with validly identified material in an herbarium. The amateur or novice bryologist has no such advantage, but that person's resource can include experienced bryologists. Unknown plants of possible interest can usually be sent to such an experienced bryologist. Typically such plants should be sent as duplicate well-labeled specimens intended as gifts in exchange for identification.

The vocabulary of bryology diverges greatly from that of vascular plant morphology. Therefore, a glossary is an essential part of any process of learning bryophyte taxonomy. Fortunately, there is a book that we can recommend highly. This book (Malcolm and Malcolm 2000) is almost always accurate and is essentially complete in presenting the special vocabulary of bryology with full illustrations in color. This book is readily available in North America, and is distributed through Timber Press, as well as most bookstores.

A few words or expressions appear in our keys that are absent or inadequately described in Malcolm and Malcolm (2000). We treat these in the discussions in the species keys. The list below should allow reference to the appropriate discussions when the worker is unable to receive satisfaction from use of the glossary in Malcolm and Malcolm (2000).

Gametophyte Characters:

Growth Form:

Plumose vs. Dendroid: see *Climacium*

Plagiotropic/Orthotropic Shoots: see *Plagiomnium*

Leaf Lamina:

Nematogons: see *Calliergon*, *Hookeria*

Cuticular Papillosity: see *Amphidium*

Channeled Leaves: see *Didymodon*

Carinate Leaves: see *Fontinalis*

Cell Corner Thickening: see *Mnium*

Chlorocysts/Hyalocysts: see *Sphagnum*

Postical/Antical Margin: see *Schistostega*

Leaf Margin:

Crassiserrulate, Crassidentate, etc.: see *Ditrichum*

Binate vs. Geminate: see *Conardia*

Costa Morphology:

Hydroids: see *Syntrichia*

Stereid Bands: see *Campylopus*

Stem Morphology:

Brachytheciaceae Pseudoparaphyllia: see *Amblystegium*

Macronematal Apparatus: see *Anacolia*

Micronemata/Macronemata: see *Rhizomnium*

Leaf Buttress: see *Bryum*

Hyaloderm: see *Hypnum*, *Sanionia*

Axillary Hairs: see *Leptobryum*

Sexuality: see *Atrichum*

Sporophyte Characters:

Funarialean Peristome: see *Entosthodon*

Funarialean Stomates: see *Entosthodon*

Cryptoporous/Phaneroporous Stomates: see *Orthotrichum*

EVOLUTION OF THESE KEYS

The present work has had a long gestation period with many persons contributing to the design of the keys. The keys trace to early use in classes in bryology at Humboldt State University (1967–1993). Early versions of the key allowed students to identify mosses likely to be encountered in the *Sequoia* forest belt of northwest California. Over time additional taxa were added with the key expanded to accommodate the mosses then recorded for all of the state.

After retirement from Humboldt State the senior author began further to develop the keys, and the

junior author added his organizational skills and his knowledge of the southern portions of the state. We worked together in close partnership—a partnership enabled by Dr. Brent Mishler of the University of California, Berkeley. Our mutual interest in bryogeography and floristics led to a vouchered catalogue of California mosses and their distribution in the state. This catalogue has become the basis for the current version of the keys. Thousands of specimens have been examined at Berkeley, and the junior author added the data from his examination of mosses from other herbaria.

While work progressed on the California moss catalogue, bryophyte identification courses were taught through the Jepson Workshop Series. These workshops provided opportunity for their use and improvement by professional botanists and by native plant enthusiasts.

These teaching experiences taught us that keys alone were inadequate even for botanists whose primary emphasis was in phanerogams. The keys as they appear in this manuscript include introductory paragraphs and diagnostic features, as well as a discussion of ecology and habitat parameters of some of the genera and species. We have in recent years added at least one species every month to the known state flora, and that fact has suggested that the keys be expanded to include materials from all of the surrounding states as well as Washington.

These keys are further viewed as the basis for a future flora with all species described. It is our hope that this and future works provide a catalyst for botanists and plant enthusiasts to learn more about California mosses.

KEY ORGANIZATION AND DESIGN

In bryofloras, keys are generally of two types. The first set of keys provides recognition to families, with identification to genera and species relying on a second tier of keys. While the present keys seem to represent the same overall organization, such similarities are only superficial. Here, instead, we take an approach adapted to amateurs and plant enthusiasts for whom family recognition is not intuitive. Established bryologists will often be surprised to find phylogenetically unrelated plants in some of the genus keys. We do this based upon our experience in teaching various moss identification courses, and so we stress “similarity of characters” without regard to presumed phylogeny. The so-called “General Key” keys to “morphologically similar clusters,” not to families, and the “Species Keys” (the second unit in this manuscript) are simply arranged in alphabetical order by a genus name representing each morphologic cluster. Those persons familiar with moss families and genera can proceed directly to the applicable genus for species identification, thereby bypassing the general key. Botanists interested in the hierarchical classification of mosses can access that classification as presented in Buck and Goffinet (2000) in Appendix I.

GENERAL KEY

The “general key” (pages 135–148) is the route to a large number of “species keys,” the second unit in this manuscript. A novel feature of the general key is a listing of the species that fall out in each terminal dichotomy. Once a specimen has been routed to the end of a terminal dichotomy, one can proceed to the principal genus as cited for identification to species. The general key, like the species keys, is highly redundant and will often allow correct determination along several routes through the key.

Each of the “species keys” opens with a listing of the primary morphological characters of the included plants. Also included is a listing of the species covered by that key. The species list includes both names and authorship of those names. Each species key includes all the California species of the genus, and it includes all species of adjacent states, except Arizona. Exclusion of species of Arizona is necessary because of the large Rocky Mountain element in the flora of eastern parts of that state. Many moss species covered in the species keys remain unknown from California and those are indicated throughout the text by an asterisk (*). Appendix II provides a listing of those not-yet-in-California mosses in a defined order (Oregon, Washington, Nevada and Baja California Norte).

- A. Gametophyte essentially absent; plant visible as a large sporophyte (8 mm or more high) with a papillose seta and an asymmetric, capsule on an erect seta; restricted to rotten logs or highly organic soil. *Buxbaumia*: *B. aphylla*, *B. piperi*, *B. viridis*
- A. Not as above. B
- B. Leaves ecostate (plants considered to be ecostate usually have a short double costa that extends only a few cells above the leaf insertion; only a few cannot be shown to have a costa), or doubly costate with neither branch extending much above mid-leaf. C
- B. Leaves uncostate (plants considered uncostate generally have that costa extending to mid-leaf or beyond but sometimes that costa ends slightly below mid-leaf; some uncostate mosses have accessory short costae on each side of the main costa; some uncostate mosses may have that costa with short forks near its distal end). AH

- C. Leaves with hyaline awns; leaves deeply concave. D
- C. Leaves without hyaline awns; leaves various, mostly not concave. F
- D. Plant erect and unbranched; central portion of leaf with photosynthetic filaments; capsules arranged on long and straight setae. *Aloina*: *A. bifrons*, *A. roseae**
- D. Plant prostrate and extensively branched central portion of leaf without photosynthetic lamellae; setae long or short. E
- E. Median cells strongly papillose; leaves longer than 1 mm; capsules mostly immersed on short lateral branches. *Hedwigia*: *Braunia secunda**, *Hedwigia ciliata**, *H. detonsa*, *H. stellata*, *Pseudobraunia californica*
- E. Median cells smooth; leaves very small, seldom more than 0.5 mm long; capsules exserted. *Lescuraea*: *Iwatsukiella leucotricha**
- F. Median and upper leaf cells papillose or prorate. G
- F. Median and upper leaf cells smooth or, at most, with a few of the cells near the apex sparingly prorate. K
- G. Reddish to blackish erect and essentially unbranched plant growing in cushions on exposed siliceous rocks. *Andreaea*: *A. alpestris*, *A. rupestris*
- G. Plant extensively branched and mostly prostrate to decumbent or forming pinnate axes which may be partially ascending. H
- H. Paraphyllia present and obvious, especially on main stem axis. I
- H. Paraphyllia absent or leaf-like; branching not as above. J
- I. Plant regularly many times pinnately branched with the branches arranged in a single plane; leaves of branches markedly differentiated from those of the main stem. *Hylocomium*: *Hylocomium splendens*
- I. Plant sparingly and irregularly branched; branch and stem leaves very similar. *Lescuraea*: *Pterigynandrum filiforme*
- J. Costa double with both branches reaching nearly to mid-leaf; leaves large, mostly more than 4 mm long. *Hylocomium*: *Rhytidiadelphus triquetrus*
- J. Costa absent or short; leaves smaller. *Heterocladium*: *H. dimorphum*, *H. macounii*, *Myurella julacea*, *Pseudoleskeella tectorum*
- K. Plant complanate-foliate. L
- K. Plant not at all complanate. S
- L. Leaves strongly undulate, serrate near apex with the distal teeth on some of the leaves curled back and pointing toward the leaf base. *Neckera*: *N. douglasii*
- L. Leaves entire to serrulate or, if somewhat serrate, the teeth not recurved and the leaves not undulate. M
- M. Median leaf cells mostly over 50 μ m broad; leaf apices obtuse to broadly acute; nematogons present at leaf apices. *Hookeria*: *H. acutifolia**, *H. lucens*
- M. Median leaf cells more narrow or the leaf without nematogons in the apical region. N
- N. Interior basal cells strongly porose; at least some leaves of the stem tips with serrate apices. *Hypnum*: *Herzogiella seligeri*, *H. striatella*
- N. Interior basal cells not porose; leaves entire to serrulate. O
- O. Outer cortical cells of stem thick-walled and narrow-lumened, thus resembling adjacent inner cortical cells. P
- O. Outer cortical cells of stem mostly larger and thinner-walled than adjacent inner cells, not resembling inner cortical cells. Q
- P. Stem and branch leaves radically different with the stem leaves long acuminate but the branch leaves bluntly acute to almost obtuse; median cells mostly less than 5:1. *Heterocladium*: *H. procurrens**
- P. Plant essentially isophyllous; median laminal cells mostly more than 8:1. *Plagiothecium*: *Dacryophyllum falcifolium*, *Isopterygium tenerum*, *Pseudotaxiphyllum elegans*
- Q. Leaves at least somewhat concave with a short, usually forked costa or with a strong double costa; leaf apex blunt; plant aquatic or semi-aquatic. *Hygrohypnum*: *H. ochraceum*
- Q. Leaves not at all concave; costa, if present, not forked above the base; leaf apex usually acute; plant of mesic habitats. R
- R. Leaves strongly decurrent to auriculate-decurrent. *Plagiothecium*: all *Plagiothecium*, *Buckiella undulata*
- R. Leaves not decurrent; tropical plant escaped as a lawn weed in coastal cities of California. *Hypnum*: *Vesicularia vesicularis*
- S. Leaf apex blunt, obtuse or rounded, never with an apiculus or an awn. T
- S. Leaf apex acute to acuminate or subulate. Y

- T. Plant erect and unbranched, with deeply concave leaves formed by infolded leaf margins, with photosynthetic lamellae arranged along the leaf center. **Aloina**: *A. ambigua*, *A. rigida*
- T. Plant prostrate and branched, without photosynthetic lamellae on the leaves. U
- U. Leaves 3-ranked and usually so strongly carinate (except in *Fontinalis hypnoides*) as to have the two lateral halves of the leaves pressed against one another; plant aquatic. **Fontinalis**: all *Fontinalis*
- U. Leaves not 3-ranked, never strongly carinate. V
- V. Alar cells so inflated as to appear swollen and overlapping, very hyaline, these cells making a group ascending 4–10 cells up the margin and a similar distance toward the middle; stem tips with leaves so closely appressed as to appear fusiform. **Hypnum**: *Calliergonella cuspidata*
- V. Alar cells less inflated and fewer; stem and branch apices not at all fusiform. W
- W. Leaves less than 0.5 mm long, coarsely dentate, closely arranged on julaceous stems. **Heterocladium**: *Myurella julacea*
- W. Leaves larger, entire to serrulate, not julaceous. X
- X. Plant of mesic to very wet but never submerged sites, mostly pinnately branched from obvious reddish stems; alar cells quadrate and mostly somewhat thick-walled. **Hylocomium**: *Pleurozium schreberi**
- X. Plant aquatic or in constantly very wet sites, seldom pinnately branched, never with red stems; alar cells various. **Hygrohypnum**: all *Hygrohypnum*
- Y. Plant very small with larger leaves less than 1 mm long. Z
- Y. Plant and leaves larger. AD
- Z. Plant unbranched with a cleistocarpous, sessile capsule arising from a rosette of strongly serrate to fimbriate leaves; protonema usually forming a conspicuous greenish felt. **Acaulon**: *Ephemerum serratum*
- Z. Plant with stems more than 1 mm long; branched and usually prostrate; sporophyte, when present, stegocarpous. AA
- AA. Leaves dentate to fimbriate with their terminal cells abruptly several times as long as the adjacent subterminal ones. **Fabronia**: *F. ciliaris*, *F. pusilla*
- AA. Leaves with entire to serrulate or serrate margins; apical cells of leaves not so differentiated. AB
- AB. Plant julaceous. **Lescuraea**: *Pseudoleskeella serpentinensis*, *Tripterocladium leucocladulum*
- AB. Leaves spreading to loosely erect. AC
- AC. Leaves somewhat falcate-secund; costa forked distally below or near mid-leaf; cuticle often minutely verruculose. **Lescuraea**: *Leptopterigynandrum austro-alpinum*, *Pseudoleskeella tectorum*
- AC. Leaves symmetric with costa shorter and not-forked; cuticle smooth. **Amblystegium**: *Platydictya jungermannioides*
- AD. Plant whitish-green, densely fasciculate-branched; leaf cells of two forms with large, empty transparent ones alternating with small, green ones (these green cells may be so narrow as to be interpreted as the lateral walls of the transparent cells); plant restricted to very wet sites. **Sphagnum**: all *Sphagnum*
- AD. Not as above. AE
- AE. Leaves 3–6 mm long, broadly ovate, often plicate; costae two, with both extending to leaf middle or beyond. **Hylocomium**: *Rhytidiadelphus loreus*, *R. squarrosus*, *R. subpinnatus**, *Rhytidiopsis robusta*
- AE. Leaves smaller and usually ovate-lanceolate or more narrow; costae shorter. AF
- AF. Plant plumose and ascending from an inconspicuous prostrate base; alar cells very numerous, quadrate and pachydermous, extending more than 10 cells up the margin. **Antitrichia**: *Alsia californica*, *Pterogonium gracile*
- AF. Plant prostrate to ascending without strong differentiation of a prostrate main axis and an erect secondary axis; alar cells fewer and poorly differentiated. AG
- AG. Leaves squarrose but not falcate; abruptly contracted below or near the middle into a long and channeled acumen. **Campylium**: *C. hispidulum*, *C. stellatum*
- AG. Leaves not squarrose, often falcate-secund, with apices various but without a channeled acumen. **Hypnum**: all *Hypnum*, *Breidleria pratensis**, *Homomallium mexicanum*, *Isopterygiopsis pulchella*, *Ptilium crista-castrensis**, *Sematophyllum adnatum*, *Orthothecium chryseum**
- AH. Basal and sometimes all cells thick-walled with the lateral walls sinuose. **Racomitrium**: all *Racomitrium*
- AH. Cells with lateral walls not sinuose. AI

- AI. Cells papillose, cuticular papillose, strongly mammillose or evenly prorate at least in the distal one-half of the limb. AJ
- AI. Cells smooth, or with a few scattered prorate in the distal portion of the leaf. CE
- AJ. Leaves with hyaline to yellowish awns. AK
- AJ. Leaves not awned or with the awns concolorous with the adjacent apex or only slightly bleached near the distal end. AQ
- AK. Plants prostrate and much branched; costa ending before the apex and the awn composed mostly of lamina cells. *Claopodium*: *C. bolanderi*, *C. crispifolium*
- AK. Plants erect and usually little branched; or, if branched, the awn formed from the excurrent costa. AL
- AL. Costa with adaxial photosynthetic lamellae or filaments; margins plane to incurved. CU
- AL. Costa without such outgrowths. AM
- AM. Plants with multicellular gemmae obvious in leaf axils or inserted on leaf lamina; leaf margins plane or nearly so; plants usually less than 5 mm high and mostly epiphytic. *Syntrichia*: *S. laevipila*, *S. pagorum*, *S. papillosa*
- AM. Plants without such multicellular gemmae; leaf margins and plant habit various. AN
- AN. Leaf margins plane to erect, or slightly recurved near middle; awn mostly smooth; calyptra large and campanulate enveloping all the capsule. *Encalypta*: *E. brevicollis**, *E. brevipes**, *E. ciliata*, *E. procera*, *E. rhyptocarpa*, *E. vulgaris*
- AN. Leaf margin recurved at least near base or, if with plane margins, with a serrulate awn; calyptra cucullate and sheathing only distal ½ of capsule. AO
- AO. Basal cells not enlarged and thin-walled; alar cells quadrate; adaxial surface of costa covered by rectangular cells with somewhat sinuose lateral walls. *Grimmia*: *G. elatior**, *G. lesherae*, *Schistidium strictum**
- AO. Basal cells mostly large, rectangular and thin-walled without alar differentiation; adaxial surface of costa with quadrate cells similar to those of lamina. AP
- AP. Costa in cross-section with a single crescentic abaxial stereid band and mostly without a differentiated dorsal epidermis. *Syntrichia*: *S. bartramii*, *S. caninervis*, *S. laevipila*, *S. norvegica*, *S. obtusissima*, *S. papillosissima*, *S. princeps*, *S. ruralis*
- AP. Costa in cross-section with an elliptical abaxial stereid band and sometimes with a small adaxial band; epidermis of abaxial face of costa well-differentiated. *Tortula*: *T. brevipes*, *T. euryphylla*, *T. guepinii*, *T. muralis*, *Pseudocrossidium crinitum*
- AQ. Leaf margins in distal portion of leaf serrulate to dentate. AR
- AQ. Leaf margins entire throughout, or with toothing only near the base, or within a few cells of the apex. BK
- AR. Plants branched. AS
- AR. Plants unbranched or branched only by innovations, sometimes seemingly irregularly branched. AW
- AS. Plants plumosely branched with the branches somewhat elevated above the substratum; leaves not catenulate when dry. AT
- AS. Plants prostrate; leaves catenulate when dry. AV
- AT. Alar cells thick-walled and very deeply green in an explanate pocket; most of the cells in the distal portion of the leaf prorate-spinose; plant mostly pendent from tree limbs in the northwest of the state. *Isoetecium*: *I. spiculiferum*
- AT. Alar cells not so differentiated; habitat various. AU
- AU. Stems and branches with leaves julaceous; median cells prorate; alar cells quadrate, extending in a large group more than 10 cells up the leaf margin and toward the costa. *Antitrichia*: *Dendroalsia abietina*, *Pterogonium gracile*
- AU. Plants not julaceous; median cells unipapillose or pluripapillose; alar cells not uniformly quadrate. *Hylocomium*: *Helodium blandowii*, *Rhytidium rugosum**, *Thuidium recognitum**
- AV. Plants without foliose paraphyllia on stems and branches; cells of leaf margin almost without papillae; median cells centrally unipapillose. *Claopodium*: *C. whippleanum*, *Meteorium nigrescens**
- AV. Plants mostly with such paraphyllia; cells of leaf margin with similar papillosity to those of interior; median cells mostly with papillae near cell ends. *Lescuraea*: *L. incurvata*, *L. pallida*, *L. patens*, *L. radicata*, *L. saviana*, *L. stenophylla*
- AW. Leaf base differentiated with that base completely wrapped around stem, hyaline to reddish, strongly differentiated in cell shape and color from the limb. AX
- AW. Leaf base sometimes partially sheathing but never completely encircling the stem. AY
- AX. Leaves strongly mammillose with the limb rigidly appressed when dry. *Timmia*: *T. austriaca*, *T. bavarica*, *T. megapolitana**

- AX. Leaves strongly papillose or prorate-papillose with the limb often somewhat crispate. **Anacolia:** *Bartramia ithyphylla*
- AY. Marginal cells differentiated as a limbidium, either elongate or epapillose and somewhat larger than adjacent isodiametric laminal cells. **Tortula:** *T. subulata*, *Hennediella heimii*, *H. stanfordensis*
- AY. Marginal cells not differentiated in the manner described above. AZ
- AZ. Alar cells very much inflated, usually reddish in older leaves; leaves falcate-secund. **Dicranum:** *D. fuscescens*, *D. sulcatum*
- AZ. Alar cells neither inflated nor strongly colored. BA
- BA. Median cells of leaves pluripapillose; cells across the entire leaf base rectangular, thin-walled, smooth and pellucid. **Barbula:** *Barbula ehrenbergii*, *Bryoerythrophyllum recurvirostrum*
- BA. Median cells of leaves unipapillose, prorate or with cuticular papillosity; basal cells various. BB
- BB. Leaves 10:1 or more, mostly subulate with costa filling most of the apex and percurrent to excurrent. BC
- BB. Leaves broader with costa of various lengths. BG
- BC. Median cells with cuticular papillose ridges running continuously from near the base to the apex; leaves crispate when dry. BD
- BC. Median cells without such cuticular ridges; leaves crispate or not. BE
- BD. Leaf margins remotely serrate to serrulate with very small teeth right angular in outline; leaves spirally inserted, not obviously ranked. **Amphidium:** *A. californicum*
- BD. Leaf margins evenly and coarsely dentate with pointed teeth; leaves in 3 straight ranks on the stem. **Anacolia:** *Plagiopus oederianus**
- BE. Plant red-brown to almost black, growing on siliceous rock at high elevations, often below snow beds; capsules without an operculum, dehiscent by four longitudinal lines. . . . **Andreaea:** *A. nivalis*
- BE. Leaf limb symmetrical to falcate; plant green to brownish green; habitat various; capsules dehiscent by operculum. BF
- BF. Leaf margins recurved; older portion on stem with dense red-brown, papillose rhizoids inserted in a halo around the macronematal apparatus. **Anacolia:** *A. baueri*, *A. laevisphaera*, *A. menziesii*, *Bartramia pomiformis*, *B. stricta*, *Plagiopus oederianus**
- BF. Leaf margins plane to incurved; rhizoids smooth, not densely inserted and inserted around the macronematal apparatus. **Ditrichum:** *Distichium capillaceum*, *Distichium inclinatum*, *Ditrichum heteromallum*, *Ditrichum schimperii*, *Trichodon cylindricus*
- BG. Leaves bistratose with cells high mammillose only on adaxial surface; plant of low to mid-elevation, mostly disturbed soils. **Timmia:** *T. anomala*, *T. crassinervis*
- BG. Leaves unistratose with cells papillose, mammillose or prorate. BH
- BH. Leaves in five distinct ranks with that ranking emphasized by the strong keeling of each leaf; plant mostly among other mosses at high elevations. **Philonotis:** *Conostomum tetragonum*
- BH. Leaves not ranked, not strongly keeled; habitat various. BI
- BI. At least some of the cells of the distal leaf margin prorate, mostly with all of the distal cells prorate; leaves lanceolate, 2.5–3.5:1; acute to acuminate at apices. . . . **Philonotis:** *P. americana*, *P. caespitosa*, *P. calcarea*, *P. capillaris*, *P. fontana*, *P. marchica*, *P. muehlenbergii*, *P. tomentella*, *P. uncinata**, *P. yezoana*
- BI. Median leaf cells mammillose to centrally unipapillose; leaves mostly ovate to elliptic, bluntly acute to obtuse at apices. BJ
- BJ. Leaf apices acute to acuminate; lower portion of plant densely covered with red rhizoids; median cells centrally unipapillose. **Aulacomnium:** *A. androgynum*, *A. palustre*
- BJ. Leaf apices bluntly acute to rounded; lower portion of plant not densely covered with rhizoids; median laminal cells mammillose or papillose on cellular mammillosities. **Dichodontium:** *Dichodontium flavescens*, *D. olympicum*, *D. pellucidum*, *Cynodontium strumulosum**
- BK. Leaf margins plane to ascending or incurved, not recurved or with inconspicuous recurvature near the middle. BL
- BK. Leaf margins recurved, at least near the base. BS
- BL. Plant prostrate and branched; paraphyllia numerous, foliose. **Lescurea:** all *Lescurea*, *Leskea polycarpa*
- BL. Plant erect and sparsely or not at all branched; paraphyllia absent. BM
- BM. Papillae primarily of cuticular origin and thus not conforming positionally to cell outlines when viewed on leaf whole-mount. **Amphidium:** *A. lapponicum*, *Dicranoweisia contermina*
- BM. True papillae present. BN

- BN. Leaves ending in a uniseriate awn that may be bleached but is not truly hyaline; plants almost strictly epiphytic in California. *Ulota*: *Ulota megalospora*, *Zygodon rupestris*
- BN. Leaves variously acute or acuminate to obtuse at apex, never uniseriate at apex; ecology various. BO
- BO. Plant with elliptic-oblong leaves broadly rounded toward the apex; dry leaves not or little distorted, not truly crispate. BP
- BO. Plant with lanceolate leaves acute to acuminate at apex; dry leaves crispate or not. BQ
- BP. Median leaf cells pluripapillose; basal cells rectangular and inflated with transverse walls thin but with lateral walls somewhat thick and pigmented yellow to orange or reddish. *Encalypta*:
*Encalypta affinis**, *E. intermedia*, *E. procera*, *E. vulgaris*
- BP. Median leaf cells pluripapillose or unipapillose; basal cells rectangular and thick-walled, not pigmented but with some sinuosity on lateral walls. *Orthotrichum*: *O. bolanderi*,
O. obtusifolium
- BQ. Basal cells of leaf very much inflated and rectangular, extending upward along margin significantly farther than in the juxtacostal region; the margin between the laminal and basal cells thus describing a V-shape. *Tortella*: *T. alpicola*, *T. fragilis*, *T. tortuosa*
- BQ. Basal marginal cells not extending distally with those basal cells not describing a "V." BR
- BR. Margin strongly inrolled or infolded when dry; cells of limb rather uniform in size and shape. *Weissia*: all *Weissia*, *Oxystegus tenuirostris*, *Plaubelia sprengelii**,
Trichostomum brachydontium, *T. crispulum*, *T. sweetii*
- BR. Margin plane to erect; cells of strongly variable size and shape throughout the leaf limb. *Gymnostomum*: *Anoetangium aestivum**, *Eucladium verticillatum*,
*Gymnostomum aeruginosum**, *G. calcareum*, *Molendia sendtneriana*, *Zygodon rupestris*
- BS. Leaves with an obvious limbidium, either of elongate cells or differentially sized cells. BT
- BS. Leaves without a limbidium. BV
- BT. Limbidium formed of abruptly elongate cells. *Tortula*: *T. subulata*
- BT. Limbidium formed of cells larger, more pachydermous, or less papillose cells. BU
- BU. Plant large with leaves mostly more than 3 mm long; limbidium formed of one or several rows of larger and thicker, often reddened cells; plant usually growing in calcareous seeps. *Scouleria*: *Crumia latifolia*
- BU. Plant smaller with limbidium formed of one or several rows of epapillose and more pellucid cells; plant of temporarily moist soil. *Syntrichia*: *S. bolanderi*, *S. amplexa*
- BV. Plants less than 3 mm high with the leaves closely inserted; costa percurrent to excurrent. BW
- BV. Plants mostly larger, not bulbiform. BX
- BW. Median cells with obvious C-shaped papillae; plant strongly bulbiform with an essentially sessile capsule. *Acaulon*: *Phascum cuspidatum*
- BW. Median cells with numerous papillae that appear round in surface view; plant bulbiform but with capsule emergent to exserted. *Microbryum*: all *Microbryum*
- BX. Papillae cuticular and therefore seen as low ridges that frequently extend across boundaries between adjacent cells; leaves when dry spirally coiled into several turns from apex to base. *Amphidium*: *A. mougeotii*; *Grimmia anomala*
- BX. Leaves with true papillae; mostly with dry leaves not spirally coiled. BY
- BY. Adaxial surface cells of costa rectangular with sinuose lateral walls; immediate suprabasal cells near costa strongly porose; some leaves in clone often with a hyaline awn. *Grimmia*:
G. lesherae
- BY. Adaxial surface cells of costa various in shape but never with sinuose lateral walls; suprabasal cells near costa various; leaves mostly not with hyaline awns. BZ
- BZ. Costa homogeneous; papillae few, mostly high and sharp; capsules short elliptic, often sulcate; calyptra campanulate, usually hairy and plicate. *Orthotrichum*: *O. affine*, *O. alpestre*,
*O. anomalum**, *O. consimile*, *O. cupulatum*, *O. diaphanum*, *O. euryphyllum*, *O. flowersii*,
O. hallii, *O. laevigatum*, *O. lyellii*, *O. macounii*, *O. pallens*, *O. papillosum*, *O. pellucidum*,
O. praemorsum, *O. pulchellum*, *O. pumilum*, *O. pylaesii*, *O. rivulare*, *O. rupestre*, *O. shevockii*,
O. speciosum, *O. spjutii*, *O. striatum*, *O. tenellum*, *O. texanum*, *O. underwoodii*,
Ulota megalospora, *U. obtusiuscula*, *U. phyllantha*
- BZ. Costa with at least a dorsal stereid and sometimes also with a ventral one; papillae low and numerous, obscuring the lumen; capsules longer cylindric, not sulcate; calyptra mostly cucullate. CA
- CA. Leaves elliptic to broadly ovate; costa cross-section without an adaxial stereid band and with abaxial stereid band lunate, without either an abaxial or an adaxial epidermis. CB
- CA. Leaves narrowly ovate to lanceolate; costa often with two stereid bands; abaxial stereid band elliptic. CC

- CB. Leaf margins revolute in more than one complete spiral; hydrated plants with a distinct pin-wheel appearance. **Didymodon**: *Pseudocrossidium obtusulum*
- CB. Leaf margins plane to incurved or recurved; hydrated plants otherwise. **Syntrichia**:
S. latifolia; **Tortula**: *T. atrovirens*, *T. inermis*, *T. obtusifolia*
- CC. Central strand absent in stem cross-section; juxtacostal cells of median leaf slightly elongate, mostly with small trigones; peristome absent with operculum usually systylious.
. **Gymnostomum**: *Hymenostylium recurvirostre*
- CC. Central strand usually present in stem cross-section; juxtacostal cells of median leaf similar to other median laminal cells; peristome present, mostly long and spirally twisted. CD
- CD. Cell lumina tending to be quadrate with the walls equally thickened throughout; papillae low and not obscuring the cell outlines, usually four or more per cell; axillary hairs with a basal brown cell; leaf apex mostly acute, often narrowly so; costa with at least a strong dorsal stereid.
. **Didymodon**: *Bryoerythrophyllum columbianum*, *B. recurvirostre*;
Didymodon australasiae, *D. brachyphyllum*, *D. eckeliae*, *Didymodon fallax*, *D. ferrugineus*,
D. insulanus, *D. nevadensis**, *D. nicholsonii*, *D. norrisii*, *D. occidentalis*, *D. revolutus*,
D. rigidulus, *D. tectorum**, *D. tophaceus*, *D. umbrosus*, *D. vinealis*, *Triquetrella californica*
- CD. Cell lumina rounded to elliptic; papillae either numerous and obscuring the cell outlines, or few and sharp, sometimes inconspicuous; axillary hairs pale throughout; apices and stereids various. **Barbula**: *B. convoluta*, *B. ehrenbergii*, *B. eustegia*, *B. orizabensis**, *B. unguiculata*
- CE. Immediate leaf marginal cells long and narrow in one or more rows abruptly set off from the shorter cells within. CF
- CE. Leaves elimbate or with an intramarginal limbidium, or with the limbidium of short cells differentiated in cell thickness. CR
- CF. Leaves arranged in two vertical ranks with the leafy plant thus appearing flat; leaf or its base with the lamina split into two flaps that pocket the stem like the base of an *Iris* leaf. . . **Fissidens**:
F. bryioides, *F. crispus*, *F. curvatus*, *F. minutulus*, *F. sublimbatus*, *F. ventricosus*
- CF. Leaves mostly spirally inserted (if distichous, without the ampliate-clasping aspect of a *Fissidens*). CG
- CG. Limbidium intramarginal, several cells thick, with short cells like those of the median lamina to the outside of the elongate cells. **Amblystegium**: *Limbella fryei**
- CG. Limbidium marginal, often only one cell in thickness. CH
- CH. Plant dendroid with the deltoid-triangular, almost echlorophyllose stem leaves contrasting sharply with the ovate, strongly chlorophyllose branch leaves. **Plagiomnium**:
Leucolepis acanthoneura
- CH. Plant not dendroid. CI
- CI. Plant very small, with sporophyte immersed and capsule almost globose; growing as a winter and spring ephemeral on open, mostly disturbed soil. **Acaulon**: *Aphanorrhagma serratum**
- CI. Plant small to large but with sporophyte exserted and cylindrical; time and duration of growth various. CJ
- CJ. Margin geminate-dentate. CK
- CJ. Margin entire or with the teeth singly placed. CL
- CK. Leaves with vertical photosynthetic lamellae on costa; lamina frequently spinose-dentate on surface. **Atrichum**: all *Atrichum*
- CK. Leaves without photosynthetic lamellae; lamina never with surface teeth except as associated with injury during development. **Mnium**: *M. ambiguum**, *M. arizonicum*,
M. blytii, *M. marginatum*, *M. spinulosum*, *M. thomsonii*
- CL. Median leaf cells primarily quadrate to short rectangular; leaves strongly comose on the short stem; capsule sulcate with operculum dome-shaped. CM
- CL. Median leaf cells primarily elongate-hexagonal; capsules smooth with operculum apiculate. CO
- CM. Capsules inclined, often sulcate; endostome and exostome present. **Funaria**:
Funaria calvescens, *F. hygrometrica*, *F. microstoma*, *F. muehlenbergii*
- CM. Capsules erect, smooth; endostome usually reduced; exostome present or absent. CN
- CN. Exostome present, often inconspicuous (if possible, remove operculum from young capsules); exothelial cells oblong; calyptra cucullate, loosely inflated around capsule. **Entosthodon**:
E. attenuatus, *E. bolanderi*, *E. californicus*, *E. drummondii*, *E. fascicularis**, *E. kochii*,
*E. planoconvexus**, *E. rubrisetus*, *E. tucsoni*
- CN. Peristome absent; exothelial cells irregular, mostly somewhat hexagonal; calyptra mitrate to campanulate. **Physcomitrium**: *P. californicum*, *P. collenchymatum*, *P. hookeri*,
*P. pygmaeum**, *F. pyriforme*
- CO. Plant with erect perigonial and perichaetial shoots contrasting sharply with the plagiotropic

- (complanate) vegetative shoots, if without plagiotropic shoots, the marginal teeth long and sharply dentate and the costa without stereid bands. **Plagiomnium**: *P. cuspidatum*, *P. drummondii**, *P. ellipticum*, *P. insigne*, *P. medium*, *P. rostratum*, *P. venustum*
- CO. Plant without plagiotropic shoots; margin entire to serrulate, sometimes serrate. CP
- CP. Median laminal cells elongate-hexagonal to rectangular with angular end-walls, mostly more than 4:1; leaves of dorsal portion of leaning stems markedly narrower and shorter than more lateral leaves. **Pohlia**: *Epipterygium tozeri*
- CP. Median laminal cells mostly shorter than 4:1; leaves of erect stems without a dorso-lateral heterophylly. CQ
- CQ. Leaves broadly rounded to apiculate at apex, 1.5–4:1, mostly more than 3 mm long; margin multistratose at least in part. **Rhizomnium**: *R. glabrescens*, *R. gracile**, *R. magnifolium*, *R. nudum**, *R. pseudopunctatum*, *R. punctatum*, *Mnium blyttii*
- CQ. Leaves with apices mostly acute to acuminate, if rounded to apiculate, with margin unistratose or leaves smaller or more narrow. **Bryum**: *B. algovicum*, *B. amblyodon*, *B. arcticum**, *B. badium*, *B. bimum*, *B. caespiticium*, *B. calobryoides*, *B. canariense*, *B. capillare*, *B. cyclophyllum*, *B. elegans*, *B. erythroloma*, *B. flaccidum*, *B. knowltonii**, *B. laevifolium*, *B. lisae*, *B. meesioides*, *B. pallens*, *B. pallescens*, *B. pseudotriquetrum*, *B. schleicheri**, *B. torquescens*, *B. turbinatum*, *B. uliginosum*, *B. weigelii*, *Brachymenium exile**, *Brachymenium systylium**, *Roellia roellii*
- CR. Leaves two-ranked, keeled at the base, mostly ampliate clasping at the base in the manner of an iris stem. **Fissidens**: *F. adianthoides*, *F. aphelotaxifolius*, *F. asplenioides**, *F. dubius*, *F. fontanus*, *F. grandifrons*, *F. osmundioides**, *F. pauperculus*, *F. taxifolius*, *F. taylorii*, *Bryoxiphium norvegicum**, *Distichium capillaceum*, *D. inclinatum*, *Schistostega pennata**
- CR. Leaves inserted in more than 2 ranks, mostly not obviously ranked. CS
- CS. Leaves with adaxial vertical photosynthetic lamellae or filaments over the costa or over both the costa and the lamina. CT
- CS. Leaves without such adaxial lamellae. CZ
- CT. Leaves mostly very coarsely toothed; if with entire leaves those leaves mostly more than 3 mm long. CU
- CT. Leaves entire to serrulate; plant and leaves much smaller. CX
- CU. Photosynthetic lamellae mostly fewer than 12, covering only a small portion of the upper leaf lamina; plants strongly crispate when dry. **Atrichum**: *Bartramiopsis lescurei**, *Oligotrichum aligerum**, *O. hercynicum**, *O. parallellum**
- CU. Photosynthetic lamellae mostly more than 20, covering nearly all the upper leaf lamina; plants mostly not very crispate. CV
- CV. Distal cells of photosynthetic lamellae papillose or cuticular papillose. **Pogonatum**: *Meiotrichum lyallii*, *Pogonatum dentatum**, *Pogonatum urnigerum**, *Polytrichastrum alpinum*
- CV. Distal cells of photosynthetic lamellae smooth. CW
- CW. Leaves strongly crispate when dry. **Pogonatum**: *Pogonatum contortum*
- CW. Leaves not at all crispate. **Polytrichum**: *Polytrichum commune*, *P. formosum*, *P. juniperinum*, *P. longisetum*, *P. piliferum*, *P. sexangulare*, *P. strictum*
- CX. Leaf margins erect from near the base, cucullate at apex; leaves mostly without hyaline awns; cushion of photosynthetic filaments seemingly filling most of leaf concavity. **Aloina**: *A. ambigua*, *A. bifrons*, *A. rigida*, *A. roseae**
- CX. Leaf margins recurved or erect but not at all cucullate; leaves almost always with hyaline awns; photosynthetic filaments or lamellae not obscuring the bulk of the leaf lamina. CY
- CY. Leaves deeply concave with margins almost never with recurvature and with 3–5 photosynthetic lamellae narrowly inserted over costa. **Pterygoneurum**: *P. californicum*, *P. lamellatum*, *P. ovatum*, *P. subsessile*
- CY. Leaves not concave with margins recurved near base or nearly to apex; photosynthetic filaments present over costa. **Crossidium**: *C. aberrans*, *C. crassinerve*, *C. seriatum*, *C. squamiferum*
- CZ. Plants very small and essentially stemless with the closely crowded leaves forming a bulbiform cluster; costa percurrent to excurrent with the distal cells of the lamina and costa forming a somewhat bleached to almost hyaline awn; leaf cross-section with the abaxial walls of the laminal cells markedly more thick-walled than those of the adaxial surface. **Stegonia**: *S. hyalinotricha*, *S. latifolia*, *S. pilifera*
- CZ. Plants not in all respects as above. DA
- DA. Leaves with hyaline awns. DB
- DA. Leaves without hyaline awns or with the distal half of the leaf bleached and hyaline, thus appearing awned. DE

- DB. Costa filling half or more of leaf base. *Campylopus*: *C. atrovirens**, *C. introflexus*,
*C. pilifer**, *C. schmidii*
- DB. Costa more narrow. DC
- DC. Adaxial cells of costa at and above mid-leaf rectangular with at least some sinuosity on the lateral walls; leaves asymmetric with rows of cells on each side of costa differing in number. DD
- DC. Adaxial cells of costa quadrate or rectangular, not sinuose on lateral walls; leaves symmetric with rows of cells on each side of the costa equal in number. DE
- DD. Leaves with numerous quadrate cells at the alar region; sporophytes systylious and immersed; plant primarily of seasonally wet to submerged sites, often in sheet drainage; plant coloration typically with a reddish wash.
. *Schistidium*: *S. cinclidodonteum*, *S. confertum*, *S. flaccidum*, *S. tenerum*
- DD. Leaves with few or no quadrate cells in the alar region, instead with cells mostly rectangular with thickened end-walls; sporophytes immersed or exerted but never systylious; plant primarily of rock faces and boulders, generally dry; plant coloration typically green to black.
. *Grimmia*: *G. alpestris*, *G. americana**, *G. anodon*, *G. arcuatifolia*, *G. caespiticia*,
*G. donniana**, *G. elatior**, *G. hartmanii**, *G. incurva**, *G. laevigata*, *G. leibergii*,
G. lesherae, *G. lisae*, *G. longirostris*, *G. mariniana*, *G. montana*, *G. moxleyi*, *G. nevadensis*,
G. orbicularis, *G. ovalis*, *G. pilifera**, *G. plagiopodia*, *G. poecilostoma*, *G. pulvinata*,
G. reflexidens, *G. serrana*, *G. shastae*, *G. tergestina*, *G. torquata*, *G. trichophylla*,
G. ungeri, *Coscinodon calyptratus*, *C. cribrosus**, *Jaffueliobryum raui*, *J. wrightii*
- DE. Leaves more than 10:1, with the costa percurrent to excurrent, often filling the long and narrow apex; plant erect and essentially unbranched. DF
- DE. Leaves broader or the costa shorter. DY
- DF. Leaves falcate-secund, plants green to brownish-green, mostly more than 1 cm tall. DG
- DF. Leaves not falcate-secund; or if somewhat falcate, with older plants densely coated with red-brown rhizoid and with leaves having short basal plications. DK
- DG. Plant irregularly but frequently branched, restricted to frequently flooded logs and tree bases along streams. *Dichelyma*: *Dichelyma falcatum**, *D. uncinatum*
- DG. Plant unbranched except for innovations; growing in various habitats. DH
- DH. Outer cortical cells of stem strongly inflated and therefore abruptly differentiated from adjacent inner cells; plant mostly with a hint of falcate-secund expression. . . . *Orthodontium*: *O. gracile*,
O. pellucens
- DH. Outer cortical cells not so enlarged and differentiated. DI
- DI. Alar cells inflated, often red-brown; cells of alar region bistratose. *Dicranum*:
*Dicranum fragilifolium**, *D. howellii*, *D. majus**, *D. pallidisetum**, *D. polysetum**,
*D. rhabdocarpum**, *D. scoparium*, *D. spadiceum**
- DI. Alar cells not inflated; cells of alar region unistratose. DJ
- DJ. Costa without stereids in cross-section; plant primarily growing on rocks mainly in alpine regions. *Kiaeria*: *Arctoa fulvella*, *A. hyperborea**, *Blindia acuta*, *Kiaeria blyttii*,
K. falcata, *K. starkei*
- DJ. Costa with stereids in cross-section; plant primarily growing on soil. *Dicranella*: *D. crispa*,
D. heteromalla, *D. howei*, *D. pacifica*, *D. rufescens*, *D. subulata*, *D. varia**,
Cynodontium jenneri, *C. tenellum*
- DK. Costa filling half or more of the leaf base. DL
- DK. Costa more narrow. DM
- DL. Leaves very narrowly linear-setaceous; leaf margin plane; rhizoids abundant and papillose; axillary hairs persistent, with basal cells of those hairs vividly red to red-brown. *Meesia*:
Leptobryum pyriforme
- DL. Leaves mostly lanceolate; leaf margin erect; rhizoids few and smooth; axillary hair fugaceous, never with reddened basal cells. *Campylopus*: *Atractylocarpus flagellaceus*,
Campylopodiella stenocarpa, *Campylopus pyriformis*, *C. subulatus*,
*Paraleucobryum enerve**
- DM. Leaves crispate when dry. DN
- DM. Leaves not crispate. DP
- DN. Leaf margins entire, or with a few serrulations at immediate apex. . . . *Dicranoweisia*: *D. cirrata*,
D. contermina, *D. roellii**

- DN. Leaf margins serrate to dentate even below the immediate apex. DO
- DO. Leaf margins dentate with teeth mostly composed of more than one cell. **Ptychomitrium:**
P. gardneri, *P. serratum**
- DO. Leaf margins serrate, leaves more than 10:1. . . . **Anacolia:** *Bartramia halleriana**, *B. pomiformis*,
*Plagiopus oederianus**
- DP. Leaves distichous with base erect and limb reflexed. **Ditrichum:** *Distichium capillaceum*,
D. inclinatum
- DP. Leaves spirally inserted. DQ
- DQ. Leaves strongly squarrose with the sheathing base abruptly widened relative to the limb.
Dicranella: *D. crispa*, *D. grevilleana**, *D. schreberiana*
- DQ. Leaves not squarrose with limb and base not strongly differentiated. DR
- DR. Leaf tips fragile with most older leaves lacking those apices. **Dicranum:**
Orthodicranum tauricum
- DR. Leaf tips not so fragile. DS
- DS. Leaf margins recurved. DT
- DS. Leaf margins plane to incurved. DU
- DT. Older stems densely coated with papillose rhizoids; leaf once plicate on each side of the extreme base with that plica reflected in the leaf buttress. **Anacolia:** *A. baueri*, *A. menziesii*
- DT. Rhizoids smooth, not densely coating older stems; leaf not plicate or with plica not so reflected in the leaf buttress. **Ditrichum:** *D. ambiguum*, *D. pusillum*
- DU. Outer cortical cells of stem strongly inflated and therefore abruptly differentiated from adjacent inner cells; plant of logs and trees in the *Sequoia* forests. **Orthodontium:** *O. gracile*,
O. pellucens
- DU. Outer cortical cells mostly not enlarged as an hyaloderm, or if somewhat differentiated; plant growing on soil in open areas. DV
- DV. Capsules sessile and cleistocarpous; plant of disturbed or exposed soil. **Bruchia:**
Pleuridium acuminatum, *P. subulatum*
- DV. Capsules exserted, often stegocarpous. DW
- DW. Costa excurrent; sporophytes without a well-defined hypophysis. **Ditrichum:** *D. flexicaule**,
D. heteromallum, *D. montanum*, *D. schimperi*
- DW. Costa percurrent in a somewhat blunt apex. DX
- DX. Plant very small, growing on rock; hypophysis not obvious. **Seligeria:**
*Brachydontium olympicum**, *B. trichodes**, *Campylostelium saxicola**, *Seligeria campylopoda**,
*S. donniana**, *S. recurvata**, *Tetradontium brownianum**, *T. repandum**
- DX. Plant an ephemeral of open soil; sporophytes with an hypophysis at least as long as the urn.
Bruchia: *B. bolanderi*, *B. flexuosa*, *Trematodon boasii*
- DY. Plant erect and essentially unbranched (acrocarpous), or if branched, cells isodiametric or elongate with strongly sinuose walls. DZ
- DY. Plant extensively branched (pleurocarpous), mostly with main stems prostrate; cells mostly elongate. FH
- DZ. Leaves on both the stems and branches squarrose. EA
- DZ. Leaves not squarrose or only the stem leaves squarrose. EC
- EA. Plant aquatic in rapidly flowing streams, leaves and stems dark black. . . . **Scouleria:** *S. aquatica*,
S. marginata
- EA. Plant of wetland sites but not in rapidly flowing water; plants green. EB
- EB. Leaves very obviously tristichous; leaf base erect-spreading. **Meesia:** *M. triquetra*
- EB. Leaves spirally inserted with sheathing base and squarrose limb. **Dicranella:** *D. palustris*
- EC. Costa of mature leaf filling $\frac{1}{3}$ or more of leaf base. ED
- EC. Costa more narrow. EE
- ED. Leaves blunt at apex; margin recurved; plant of bogs. **Meesia:** *M. uliginosa*
- ED. Leaves acute by an excurrent costa that fills the subula; margin erect; plant of soil in open forests and savannahs. **Campylopus:** *C. subulatus*, *Dicranodontium denudatum**
- EE. Leaves strongly obovate-spatulate with distal portion of leaf 4–6 times as broad as leaf base; basal margin of leaf with long cilia. **Tayloria:** *Oedipodium griffithianum**
- EE. Leaf apex more narrow relative to base; basal margin of leaf without cilia. EF
- EF. Capsules erect with a vertically or laterally expanded hypophysis; leaves somewhat broadened near the apex with cells large and thin-walled. **Tayloria:** *Splachnum ampullaceum**,
*S. sphaericum**, *S. vasculosum**, *Tayloria hornschurchii**, *Tayloria lingulata**, *Tayloria serrata**,
*Tetraplodon mnioides**
- EF. Capsules and hypophysis otherwise; leaf shape and nature of cells various. EG
- EG. Leaf margin papillose-crenate; leaves somewhat spatulate. **Tortula:** *Leptophascum leptophyllum*

- EG. Leaf margin without papillose crenations; leaves mostly broadest below the middle. EH
- EH. Plants with stems almost absent and with the leaves closely arranged in a bud-like cluster; leaves broadest at the middle or below. EI
- EH. Plant with an obvious stem; leaf arrangement and shape various. EJ
- EI. Capsule sessile and cleistocarpous. *Acaulon*: *A. rufescens*, *A. triquetrum*;
Archidium alternifolium, *Archidium donnellii**, *Lorentziella imbricata*,
Physcomitrella patens, *Physcomitrella readeri*, *Physcomitrium immersum**
- EI. Capsule erect on a seta about 10 mm long, stegocarpous. *Pohlia*: *Discelium nudum*
- EJ. Plants strongly julaceous with leaves deeply concave and closely inserted. *Pohlia*:
Anomobryum julaceum
- EJ. Plants not julaceous. EK
- EK. Median and upper cells of leaf isodiametric or very short rectangular, often transversely elongate. EL
- EK. Median and upper cells of leaf predominantly more than 1.5:1. EZ
- EL. Basal cells not differentiated from median cells, all cells thick-walled and isodiametric or nearly so, with rounded lumina; most plants with very broad apical leaves forming a cup in which multicellular, disciform gemmae are placed; plant of logs and tree bases, typically with a rust-red cast in older portions. *Tetraphis*: *T. geniculata**, *T. pellucida*
- EL. At least the basal or alar cells elongate and differentiated from median cells; plants without gemma cups; plants without a rust-red cast except for occasional dense rhizoidal cushions. EM
- EM. Leaf bases sheathing or rather tightly wrapped around stem with cells of sheath markedly longer than the nearly isodiametric cells of the limb; leaf limbs lanceolate and rather coarsely dentate. *Oncophorus*: *O. virens*, *O. wahlenbergii*
- EM. Leaves not sheathing, only gradually contracted to the very narrowly ovate base. EN
- EN. Leaf margins coarsely serrulate to dentate with at least some of the teeth composed of ½ or more of a cell. *Ptychomitrium*: *P. gardneri*, *P. serratum**, *P. sinense**
- EN. Leaf margins entire or occasionally serrulate to crenulate near apex. EO
- EO. Leaves very obviously tristichous; cells somewhat elongate, smooth; plant of bogs. *Meesia*:
M. triquetra
- EO. Leaves not tristichous; cells isodiametric and somewhat mamilliose; plant of soil and rock outcrops. EP
- EP. Costa with abaxial lamellae several cells high. *Grimmia*: *G. ramondii*
- EP. Costa without abaxial lamellae. EQ
- EQ. Leaves bordered by a row of cells abruptly different in size, wall thickness, cell papillosity or pigmentation from the adjacent internal laminal cells. *Scouleria*:
Crumia latifolia, *Scopelophila cataractae*
- EQ. Leaves not so bordered. ER
- ER. Adaxial cells of costa at and above mid-leaf rectangular with at least some sinuosity on the lateral walls; leaves asymmetric with the rows of cells on each side of costa differing in number. ES
- ER. Adaxial cells of costa quadrate or rectangular, not sinuose on lateral walls; leaves symmetric with rows of cells on each side of the costa equal in number. EV
- ES. Leaves bistratose throughout. ET
- ES. Leaves mostly unistratose near costa at mid-leaf, often bistratose in several rows near margin. EU
- ET. Leaves narrowly lanceolate above an abruptly broadened base. *Grimmia*:
G. hamulosa, *G. unicolor**
- ET. Leaves without a differentiated broadened base. EU
- EU. Leaves with numerous quadrate cells in the alar region; sporophytes systylious and immersed; plant primarily of seasonally wet to submerged sites, often in sheet drainage; plant coloration typically with a reddish wash. *Schistidium*: *S. agassizii*, *S. atrichum*,
S. cinclidodonteum, *S. dupretii*, *S. maritimum*, *S. occidentale*, *S. platyphyllum*, *S. rivulare*
- EU. Leaves with few or no quadrate cells in the alar region, instead with the cells mostly rectangular with thickened end-walls; sporophyte immersed or exserted but never systylious; plant coloration typically green to black. *Grimmia*: *G. anomala*, *G. hartmanii**,
G. mollis, *G. serrana*, *G. unicolor**
- EV. Leaves elliptic to elliptic-ovate, rather broad to the apex; costa with only an abaxial stereid with that band elliptic in outline. *Tortula*: *T. californica*, *T. leucostama*,
T. mucronifolia, *T. plinthobia*, *T. protobryoides*, *T. systylia*, *T. truncata*
- EV. Leaves lanceolate, often narrowly so, if broader, than costa without stereid bands. EW
- EW. Leaf margins or all of upper leaf bistratose. EX
- EW. Leaves unistratose throughout. EY

- EX. Costa cross-section without stereid bands; plant forming low red cushions or tufts on siliceous rocks; leaves not crispate when dry; capsules without an operculum, dehiscent by longitudinal lines. **Andreaea**: *A. blytii*, *A. heinemannii*, *A. rothii*, *A. schofieldiana*
- EX. Costa with stereid bands; plant primarily on logs and tree bases near the coast; leaves crispate when dry; capsules with an operculum. **Dicranoweisia**: *D. cirrata*
- EY. Leaf margins with at least a few minute serrulations near apex; costa with two obvious stereid bands; capsules with seta more than 10 mm long, purple to red, occasionally yellow. **Ceratodon**: *C. purpureus*, *C. stenocarpus*
- EY. Leaf margins strictly entire; stereid bands absent; capsules immersed to emergent on a shorter seta, not strumose but often sulcate and strangulate. **Orthotrichum**: *O. euryphyllum*, *O. holzingeri*, *O. pumilum*, *Zygodon menziesii*
- EZ. Leaves falcate-secund with strongly differentiated quadrate and inflated alar cells; median laminal cells with thick and porose walls; distal portion of leaf somewhat undulate. **Dicranum**: *D. undulatum*
- EZ. Leaves not or only slightly falcate, without such an alar region; median laminal cells mostly thin, hardly or not at all porose. FA
- FA. Leaves spreading from an erect base; leaf margins entire or with a few serrulations near apex; median leaf cells rectangular with nearly parallel lateral walls. **Meesia**: *M. longiseta*
- FA. Leaves erect to spreading but without a differentiation of the base; leaf margins various; median leaf cells mostly rhomboidal to hexagonal but with longitudinal walls not parallel. FB
- FB. Median laminal cells narrowly rectangular with oblique end-walls, mostly less than 10 μ m in width; margin crassiserrulate at least near apex; capsule erect, with neck as long as urn. **Bruchia**: *B. bolanderi*
- FB. Median laminal cells rectangular to hexagonal or rhomboidal, mostly more than 10 μ m in width; margin various, often dentate or serrate; capsule mostly inclined to horizontal or pendulous, never with such a long and well-defined neck. FC
- FC. Leaves with a hint of falcation, blunt at apex with margins recurved and somewhat crenulate; median leaf cells rectangular, less than 8 μ m wide, thick-walled with lumen: wall ratio less than 6:1. **Dicranella**: *D. hilariana*
- FC. Leaves mostly symmetrical with apices and margins various; median leaf cells larger, rectangular or hexagonal with thin walls. FD
- FD. Median leaf cells primarily quadrate to short rectangular; leaves strongly comose on the short stem; capsule mostly sulcate with operculum dome-shaped; teeth of leaf margin when present somewhat vesicular-inflated; perigonia borne on small but elongate branches inserted at base of female branches; axillary hairs of markedly enlarged diameter toward distal end. FE
- FD. Median leaf cells primarily elongate-hexagonal; capsules smooth with operculum apiculate; teeth of leaf margin formed of equally thick-walled cells or of cells thickened at the tooth apex (crassi-serrate); perigonal position various but seldom at the end of a branch inserted at base of female branch; axillary hairs typically of equal diameter throughout. FG
- FE. Capsules inclined, often sulcate; endostome and exostome present. **Funaria**: *Funaria calvescens*, *F. hygrometrica*, *F. microstoma*, *F. muehlenbergii*, *Pyramidula tetragona*
- FE. Capsules erect, smooth; endostome usually reduced; exostome present or absent. FF
- FE. Exostome present, often inconspicuous (if possible, remove operculum from young capsules); exothelial cells oblong; calyptra cucullate, loosely inflated around capsule. **Entosthodon**: *E. attenuatus*, *E. bolanderi*, *E. californicus*, *E. drummondii*, *E. fascicularis**, *E. kochii*, *E. planoconvexus**, *E. rubrissetus*, *E. tucsoni*
- FE. Peristome absent; exothelial cells irregular, mostly somewhat hexagonal; calyptra mitrate to campanulate. **Physcomitrium**: *P. californicum*, *P. collenchymatum*, *P. hookeri*, *P. pygmaeum**, *P. pyriforme*
- FG. Leaves mostly with cells more than 4:1; costa usually with scattered prorate cells on some of the distal portion of its abaxial surface. **Pohlia**: all *Pohlia*, all *Mielichhoferia*, *Schizymenium shevockii*
- FG. Leaves mostly with cells shorter; costa almost never with abaxial prorations. **Bryum**: *B. alpinum*, *B. argenteum*, *B. barnesii*, *B. bicolor*, *B. blindii*, *B. gemmascens*, *B. gemmiferum*, *B. gemmilucens*, *B. gemmiparum*, *B. klinggraeffii**, *B. lanatum*, *B. microerythrocarpum*, *B. miniatum*, *B. muehlenbeckii*, *B. pyriferum*, *B. radiculosum*, *B. rubens*, *B. subapiculatum*, *B. tenuisetum*, *B. violaceum*, *Brachymenium spirifolium**, *Plagiobryum zierii**
- FH. Plant plumose to dendroid, with stem erect or upwardly arching. FI
- FH. Plant not dendroid or plumose. FP
- FI. Paraphyllia or paraphyllia-like rhizoids abundant on erect axis and larger branches. FJ

- FI. Paraphyllia absent. FL
- FJ. Leaves complanate and strongly undulate. *Neckera: Metaneckera menziesii*
- FJ. Leaves neither complanate nor undulate. FK
- FK. Leaves coarsely dentate at least above the middle; plant dendroid, mostly on soil; paraphyllia-like rhizoids with uniseriate cell arrangement present in parallel streaks along stem and branches. *Neckera: Climacium dendroides**
- FK. Leaves entire to serrulate; plant plumose, epiphytic; paraphyllia simple and unlobed or with lobes mostly more than one cell wide. *Antitrichia: Alsia californica*
- FL. Stem rigidly erect with branches radiating from near its apex; stem leaves small, deltoid-triangular, bleached and scale-like, radically different from the larger ovate to ovate-lanceolate branch leaves. *Plagiomnium: Leucolepis acanthoneura*
- FL. Stem mostly arching upwards from the substratum; stem leaves not radically differentiated as bleached scales. FM
- FM. Leaves strongly rugose, wet or dry; median cells mostly 6–10:1. *Hylocomium: Rhytidium rugosum**
- FM. Leaves not rugose; median cells isodiametric to short rectangular. FN
- FN. Median cells isodiametric to short rectangular or rhomboidal; leaves weakly or not at all plicate. *Neckera: Bestia longipes, Bryolawtonia vancouveriensis, Isoetechium cardotii, I. cristatum, I. stoloniferum, Thamnobryum neckeroides*
- FN. Median cells mostly more than 5:1; leaves at least somewhat plicate, at least on the stem. FO
- FO. Stem leaves strongly spreading to squarrose, broadly decurrent, markedly broader and less decurrent than branch leaves. *Kindbergia: K. oregana, K. praelonga*
- FO. Stem and branch leaves rather similar to one another, auriculate but not decurrent; median cells very strongly pitted. *Homalothecium: Trachybryum megaptulum*
- FP. Alar cells strongly inflated in a patch about as long as wide; plant of very moist to submerged sites. FQ
- FP. Alar cells not so inflated; habitat various. FS
- FQ. Costa ending at base of acumen or percurrent. *Drepanocladus: D. aduncus, D. capillifolius, D. crassicosatus*, D. polycarpus, Campylium polygamum, Cratoneuron filicinum, Palustriella commutata, P. falcata*, Warnstorfia exannulata, W. fluitans*
- FQ. Costa not so strong. FR
- FR. Leaf apex rounded to bluntly obtuse. *Calliergon: C. cordifolium*, C. giganteum*, Sarmientypnum sarmentosum*, Straminergon stramineum*
- FR. Leaf apex acute to acuminate. *Brachythecium: B. nelsonii, B. rivulare*
- FS. Quadrate alar cells very numerous, concolorous and thick-walled; plant plumose-erect from a prostrate rhizome; paraphyllia present. *Antitrichia: Alsia californica*
- FS. Quadrate alar cells otherwise; plant mostly prostrate or weakly ascending; paraphyllia various. FT
- FT. Costa extending at least to base of acumen. FU
- FT. Costa mostly ending near middle to $\frac{3}{4}$ FW
- FU. Leaves strongly squarrose with acumen well-demarcated and channeled, and with leaf margin essentially entire. *Campylium: C. chrysophyllum, C. radicale**
- FU. Leaves not squarrose. FV
- FV. Leaves mostly less than 1.0 mm long, minutely serrulate above, sometimes serrate in the perialar region. *Amblystegium: Amblystegium varium, Conardia compacta, Hygroamblystegium tenax*
- FV. Leaves larger, serrulate to serrate but without the special group of teeth in the perialar region; rhizoids smooth, not bearing gemmae. FW
- FW. Leaves narrowly ovate-lanceolate to lanceolate, more than 4:1; leaves mostly plicate. FX
- FW. Leaves broader; leaves plicate or not. FY
- FX. Leaves serrulate to serrate at least near the apex; stem never with a hyaloderm; costa of at least some branch leaves ending in an abaxial spine. *Homalothecium: H. aeneum, H. arenarium, H. fulgenscens, H. nevadense, H. nuttallii, H. pinnatifidum, Tomentypnum nitens**
- FX. Leaves entire or nearly so; if somewhat serrulate, with a prominent hyaloderm in the stem cross-section; costa never with an abaxial spine. *Drepanocladus: D. sordidus, Hamatocaulis vernicosus, Leptodictyum riparium, Sanionia uncinata*
- FY. Median cells typically less than 5:1. FZ
- FY. Median cells typically longer. GD
- FZ. Leaves bluntly rounded to obtuse at the serrulate to coarsely dentate apex. *Neckera: Bestia longipes, Homalia trichomanoides*, Porotrichum bigelovii*
- FZ. Leaves acute to acuminate, or apex entire to serrate. GA

- GA. Quadrate or isodiametric alar cells very numerous (more than ten along margin and toward costa); leaves serrate at least in the distal ½. GB
- GA. Quadrate alar cells fewer; leaves entire to serrate. GD
- GB. Costa forked or spurred near base, broad and flat at base with nematogons on its abaxial surface; margins narrowly and evenly recurved from base to near the apex. *Antitrichia*:
Antitrichia californica, *A. gigantea*
- GB. Costa not forked or forked distally only; margins plane or recurved only near the base. GC
- GC. Plant with leaves with coarsely serrate to fimbriate leaf margins, less than 1 mm long; terminal cell of leaves abruptly several times as long as the adjacent subterminal ones. *Fabronia*:
F. ciliaris, *F. pusilla*
- GC. Plant markedly larger with leaves serrulate with alternating large and smaller serrulations along the margin; terminal cell of leaves not differentiated. *Isothecium*: *I. cristatum*, *I. myosuroides*,
I. obtusatum
- GD. Plant julaceous. GE
- GD. Plant not julaceous. GF
- GE. Leaves with the adaxial surface of the costa base covered with short and thin-walled cells similar to those of the adjacent basal cells; leaf base typically not at all decurrent. *Scleropodium*:
*Cirriphyllum cirrosus**, *Pseudoscleropodium purum*, *Scleropodium californicum*,
S. cespitans, *S. colpophyllum*, *S. julaceum*, *S. obtusifolium*, *S. touretii*
- GE. Leaves with all surface cells of the basal, adaxial costa surface elongate and similar to such surface cells throughout the costa; leaves decurrent. *Brachythecium*: *B. collinum*,
Pseudoscleropodium purum
- GF. Leaves serrate from base to apex, mostly with a blunt apex; operculum long rostrate. GG
- GF. Leaves entire to serrulate or serrate only at extreme apex. GI
- GG. Plant plumosely branched with stem leaves markedly broader than branch leaves and with those stem leaves flexed away from stem in almost squarrose manner; distal cells of leaves not markedly shorter than proximal cells of leaves. *Kindbergia*: *K. oregana*, *K. praelonga*
- GG. Plant more irregularly branched, almost isophyllous and without squarrose flexing of stem leaves. GH
- GH. Distal cells of leaves markedly shorter than proximal cells of leaves; distal leaf cells not prorate. *Eurhynchium*: *E. hians*, *E. pulchellum*, *E. striatum*, *Platyhypnidium riparioides*,
Steerecleus serrulatus
- GH. Distal cells of leaves similar to those of proximal region; many distal cells of leaves dorsally prorate. *Brachythecium*: *B. bolanderi*
- GI. Leaves broadly rounded, sometimes mucronate at apex; plants of bogs and fens. *Calliargon*:
Pseudo-calliargon angustifolium, *P. trifarium**, *P. turgescens**
- GI. Leaves acute to broadly acute at apex; plants of mesic or hydric habitats but not in bogs or fens. GJ
- GJ. Margins plane, entire or sometimes with a few minute serrulations at apex; costa never ending in a spine; dry leaves loosely appressed to spreading; pseudoparaphyllia foliose but with the outermost bract inserted laterally or proximally. *Amblystegium*: *A. juratzkanum*, *A. serpens*,
A. varium, *Leptodictyum humile*, *L. riparium*
- GJ. Margins typically at least slightly recurved near base; serrulate, near the apex often coarsely so; costa frequently ending in a spine; dry leaves appressed to loosely spreading; pseudoparaphyllia foliose and so arranged that the outermost bract is inserted on the distal side of the cluster. *Brachythecium*: *B. albicans*, *B. asperrimum*, *B. calcareum*, *B. erythrorrhizon*,
B. fendleri, *B. frigidum*, *B. holzingeri*, *B. hylotapetum*, *B. leibergii*, *B. occidentale**,
B. oedipodium, *B. oxycladon**, *B. plumosum*, *B. populeum*, *B. reflexum*, *B. rutabulum*,
B. salebrosum, *B. starkei*, *B. velutinum*, *B. venustum*, *Cirriphyllum cirrosus**

SPECIES KEYS

The following set of keys is arranged in an alphabetic sequence, by the name of one of the included genera. The authorship and date of valid publication is provided for each genus covered by the species keys. Many of the keys include species from genera other than that of the title or primary genus. This approach allows a level of redundancy such that minor uncertainties in the use of the "Generic Key" (the previous section) will be clarified by the inclusion of species that may easily be confused with members of a particular genus. Genera that include only one or a few local species are regularly combined into a key that includes species of some other similar genus.

The introduction to each of the following generic keys attempts to describe characters that will help to signal the genus or the generic group. It further describes features of ecology and geography that may

help in its placement. On occasion, currently undescribed species are listed in the species key as “species A” as a place-holder for soon-to-be-described species. Genera with undescribed species that will be published elsewhere include: *Atrichum*, *Bryum*, *Homalothecium*, *Orthodicranum*, *Orthotrichum*, *Ptychomitrium*, *Schistidium*, *Scleropodium*, *Scouleria*, *Syntrichia*, and *Tortula*.

***Acaulon* C. Müller Hal., 1847.**

In the key that appears below, we have included all the essentially stemless California plants mostly with costate leaves and cleistocarpous, sessile sporophytes. All these are winter-growing species of seasonally dry soil.

Species included in this key: All Pottiaceae except *Archidium* (Archidiaceae); *Ephemerum* (Ephemera-ceae); *Aphanorhegma*, *Physcomitrella*, and *Physcomitrium* (Funariaceae); and *Lorentziella* (Gigasperma-ceae).

- Acaulon rufescens* A. Jaeger
- Acaulon triquetrum* (Spruce) C. Müller Hal.
- Aphanorhegma serratum* (W. J. Hooker. & Wilson in Drummond) Sullivant in A. Gray*
- Archidium alternifolium* (Dickson ex Bridel) Mitten
- Archidium donnellii* Austin*
- Ephemerum serratum* (Schreber ex Hedwig) Hampe
- Lorentziella imbricata* (Mitten) Brotherus
- Phascum cuspidatum* Hedwig
- Physcomitrella patens* (Hedwig) Bruch & W. P. Schimper
- Physcomitrella readeri* (C. Müller Hal.) Stone & G. A. M. Scott
- Physcomitrium immersum* Sullivant*
- Stegonia hyalinotricha* (Cardot & Thériot) Zander

The plants here included are among our smallest ephemeral mosses. Most appear as scattered individual plants, but a few produce turfs of contiguous plants. The gametophyte is almost stemless, and the few leaves allow no effective distinction between the vegetative leaves and the perichaetial leaves. Placement of *Acaulon* in the Pottiaceae may be difficult because the median cells of the leaves are elongate hexagonal and smooth (in our two species). Instead, one identifies the plant to genus by noting the erect leaves that completely sheath and hide the nearly sessile sporophytes.

- A. Leaves ecostate and strap-shaped with margins coarsely dentate; plant with a very conspicuous felt-like protonema. *Ephemerum serratum*
- A. Leaves costate, lanceolate to ovate-lanceolate with margins entire to serrulate or serrate, rarely dentate; protonema seldom obvious. B
- B. Median leaf cells mostly papillose with C-shaped papillae; abaxial walls of median laminal cells not markedly different in thickness from the adaxial walls; leaf margins mostly rather broadly recurved near the middle. *Phascum cuspidatum*
- B. Median leaf cells smooth; leaf margins plane or minutely recurved near the extreme base. C
- C. Spores larger than 100 µm in diameter. D
- C. Spores markedly smaller, mostly about 20 µm in diameter. F
- D. Costa cross-section without stereid bands; leaves appearing bleached and hyaline, at least above the middle; plant with inconspicuous rhizomatous branches arising from basal portions of the upright stem. *Lorentziella imbricata*
- D. Costa cross-section with a well-developed abaxial stereid band; leaves of healthy plants not bleached; plant without rhizomatous growths. E
- E. Median cells of larger leaves extremely variable in size and shape, often with quadrate cells adjacent to long elliptic cells; perigonia on lateral branches with fully defined bracts. *Archidium donnellii**
- E. Median cells of larger leaves uniformly short rectangular to rhombic; antheridia usually naked in axils of lower perichaetial leaves. *Archidium alternifolium*
- F. Leaves subtending the sessile sporophyte spreading and easily revealing the sporophyte whether moist or dry; median laminal cells rectangular and thin-walled. G
- F. Leaves erect around the sessile sporophyte hiding most or all of it without dissection; median laminal cells otherwise. J
- G. Capsules irregularly and tardily dehiscent; exothecial cells very thin-walled throughout. *Physcomitrella readeri*
- G. Capsules with a well-defined operculum; exothecial cells with collenchymatous or regular thickenings. H

- H. Exothecial cells strongly collenchymatous. *Aphanorrhegma serratum**
H. Exothecial cells not collenchymatous. I
I. Exothecial cells thick walled; operculum rostrate. *Physcomitrium immersum**
I. Exothecial cells thin walled; operculum conic-apiculate *Physcomitrella patens*
J. Leaves with a prominent awn, often somewhat hyaline; sporophyte immersed but not completely hidden by the enclosing perichaetial leaves. *Stegonia hyalinotricha*
J. Leaves without an awn or with that awn short and not hyaline; sporophyte so immersed as to require removal of perichaetial leaves to enable visibility. K
K. Upper (perichaetial) leaves keeled but slightly spreading so that some part of the urn of the mature sporophyte can usually be seen without dissection; plant tristichous in vertical view; seta arcuate. *Acaulon triquetrum*
K. Upper leaves closely enclosing and hiding the mature sporophyte; plant roughly pentastichous in vertical view; seta straight. *Acaulon rufescens*

Aloina Kindberg, 1882. *nomen conservandum*

Plants keyed in this section are small plants of seasonally dry soil. The plants placed in *Aloina* have deeply concave leaves whose margins are incurved. The cup-shaped leaves enclose a patch of photosynthetic filaments that are so closely placed as to appear as a deep green cushion. Smooth but more or less quadrate median laminar cells combine with an often obscure capsule to make the plant seem unusual within the Pottiaceae.

Species included in this key: all Pottiaceae

- Aloina ambigua* (Bruch & W. P. Schimper) Limpricht
Aloina bifrons (De Notaris) Delgadillo
Aloina rigida (Hedwig) Limpricht
Aloina roseae (Williams) Delgadillo*

Among California mosses, there are three genera of very small mosses with various patterns of photosynthetic processes on the adaxial surface of the costa. *Pterygoneurum* has sheets of cells (lamellae) on that costa, and these lamellae may remind one of the arrangement of the photosynthetic lamellae in the Polytrichaceae, a family of consistently larger plants. *Crossidium* and *Aloina* have a cushion of closely arranged filaments. *Aloina* is easily distinguished from *Crossidium*: the former genus has margins that inflex over, and partially obscure the cushion of photosynthetic filaments, the latter has reflexed to recurved leaf margins.

- A. Leaf with hyaline awn. B
A. Leaf muticous with costa ending before apex or percurrent. C
B. Costa cross-section lacking stereid bands, costa therefore hard to distinguish from adjacent cells. *Aloina bifrons*
B. Costa present and well-defined; stereid bands in cross-section several cells thick. ... *Aloina roseae**
C. Marginal cells of leaf base similar to adjacent interior cells. *Aloina ambigua*
C. Cells of basal margin of leaf hyaline and thin-walled, often elongate, forming a well-demarcated limbium. *Aloina rigida*

Alsia Sullivant, 1855. *see Antitrichia*

Alsia californica (W. J. Hooker & Arnott) Sullivant

Normally developed forms of *Alsia* are easily recognized by the combination of the numerous quadrate and thick-walled alar cells, the plumose habit and the abundant foliose paraphyllia. Some confusion may come from the great variability of the costa length on leaves from even a single clone. The costa may sometimes end significantly below the leaf middle, and it may sometimes extend even to $\frac{3}{4}$.

Close to the ocean shore, and especially on offshore islands, *Alsia* may be very different from the "normal form." In such sites it grows as prostrate and sparingly to irregularly branched mats. We consider this coastal expression a form unworthy of special recognition because of similar leaf and paraphyllial morphology. High in the canopy of coastal trees of *Pseudotsuga*, *Alsia* often shows a form with short upright axes and closely arranged branches. The paraphyllia of this expression are so much more narrow than those of the typical form that Manuel (1974) annotated a specimen at UC to be taxonomically distinct. We have, with hesitancy, decided to avoid separate species recognition.

Dendroalsia is somewhat similar to *Alsia* but the single species of that genus has prorate-papillose

median laminal cells; it is taller, mostly above 4 cm. The regularly 5-ranked leaves of *Dendroalsia* may be the easiest field character of distinction of a small and poorly developed specimen.

Alsia has one of the more difficult-to-explain geographic and ecological ranges. It reaches its most prolific development in coastal *Alnus* forests in the far northwest corner of the state but it virtually disappears from the forests north of the state line. *Alsia* grows on coastal sites in the far northwest of the state, and it is completely replaced by *Dendroalsia* inland of the first ridges of the coastal mountains. A recent collection of *Alsia* from Yuba County seems to be a remarkable disjunct population in the extreme northwest of the Sierra Nevada. In central and southern California, *Alsia* is the more common plant even east of the coastal mountains with *Dendroalsia* perhaps more common nearest the coast.

Amblystegium Bruch & W. P. Schimper, 1853.

The plants that we include in the following key are small (leaves mostly less than 1.5 mm long), and most have short median laminal cells and quadrate to short rectangular, never inflated alar cells. The lanceolate leaves are acuminate to acute, never plicate, and the stems either lack paraphyllia or the paraphyllia are so scarce as to be seldom noted. With the exception of *Leptodictyum riparium*, the mosses in this key have cells shorter than 5:1.

Species included in this key: all Amblystegiaceae except *Brachythecium* (Brachytheciaceae); *Conardia* (Campyliaceae); and *Platydictya* (Hypnaceae)

- Amblystegium juratzkanum W. P. Schimper
- Amblystegium serpens (Hedwig) Bruch & W. P. Schimper
- Amblystegium varium (Hedwig) Lindberg
- Brachythecium bolanderi (Lesquereux) A. Jaeger
- Conardia compacta (C. Müller Hal.) H. Robinson
- Hygroamblystegium tenax (Hedwig) Jennings
- Leptodictyum humile (Palisot de Beauvois) Ochyra
- Leptodictyum riparium (Hedwig) Warnstorf
- Limbella fryei (R. S. Williams) Ochyra*
- Platydictya jungermannioides (Bridel) H. Crum

Amblystegium is a genus of small to medium-sized pleurocarpous mosses of moist to aquatic sites. It is the type genus of the traditional family Amblystegiaceae that has been further divided by modern workers. Three new families concern us in California. Two of these differ from the narrowed Amblystegiaceae in the presence of paraphyllia: the Cratoneuraceae and the Helodiaceae. The third family, Campyliaceae, includes a number of generally larger plants with falcate or squarrose or reflexed, often plicate leaves, often with hyaloderm layers on the stems, and often with blunt apices. None of these latter features characterizes the plants in the present key. The Amblystegiaceae in the older sense included the majority of the pleurocarpous and costate mosses of aquatic to semi-aquatic sites. These were contrasted with the similar mosses of mesic sites, the Brachytheciaceae. More recent work by Ignatov and Huttunen (2002) allows close morphological definition of the Brachytheciaceae relative to the Amblystegiaceae *sensu lato*. Both these families have foliose pseudoparaphyllia but the outermost bract is inserted laterally or proximally in the Amblystegiaceae while the Brachytheciaceae has it inserted on the distal side of the pseudoparaphyllial cluster.

- A. Costa very strong, ending at least in the base of the acumen. B
- A. Costa absent or shorter. F
- B. Leaves with a prominent border of elongate and thick-walled cells arranged as multistratose limbidium that resembles an additional two costae. Limbella fryei*
- B. Leaf border undifferentiated or consisting only of slightly more elongate cells. C
- C. Leaf serrate to serrulate at base, often with the corners of two adjacent cells contributing to a single tooth; rhizoids typically papillose. Conardia compacta
- C. Leaf entire or distally minutely serrulate; rhizoids smooth. D
- D. Median leaf cells mostly more than 15:1; leaves 2–4 mm long, inserted somewhat obliquely on the stem. Leptodictyum riparium
- D. Median leaf cells 2–6:1; leaves mostly less than 1.5 mm long, inserted transversely on the stem. E
- E. Costae of most leaves broadened at the base and tapering above, filling about ¼–½ of leaf base, percurrent to short-excurrent; leaves with 2–3 rows of enlarged, short rectangular to elliptical cells at their insertion and below the numerous quadrate alar cells. Hygroamblystegium tenax
- E. Costa more narrow, typically ending before the leaf apex or percurrent; leaves with only a single row of such enlarged cells at insertion. Amblystegium varium

- F. Alar cells gradually shorter than median laminal cells but remaining rectangular and not at all well-defined. G
- F. Alar cells quadrate to short-rectangular or inflated, forming a rather abruptly defined group at cell angles. H
- G. Leaves on at least some stems obliquely attached and asymmetric; median leaf cells mostly more than 10:1; plant usually in slow-flowing or stagnant water. *Leptodictyum riparium*
- G. Leaves all transversely attached and symmetric; median leaf cells less than 10:1; plant usually on soil or logs on stream sides. *Leptodictyum humile*
- H. Leaves seldom exceeding 1 mm in length; costa essentially absent. *Platydictya jungermannioides*
- H. Leaves larger; costa mostly extending to mid-leaf. I
- I. Leaf margins strongly serrate nearly to base; some of the upper leaf cells with distal prorations. *Brachythecium bolanderi*
- I. Leaf margins entire or weakly serrate above the middle; none of the distal leaf cells with prorations. J
- J. Leaves erect to erect-spreading with the angle between leaf and stem seldom exceeding 30°; alar cells quadrate. *Amblystegium serpens*
- J. Leaves widely spreading (leaf/stem angle exceeding 45°); alar and basal cells rectangular and wider than upper cells. *Amblystegium juratzkanum*

***Amphidium* W. P. Schimper, 1856.**

The mosses in this key are acrocarpous plants with very narrow and strongly crispate leaves with cuticular papillosity on the essentially isodiametric cells of the lamina. Papillae formed from such sculpturing of the cuticle are uncommon among California mosses with possible confusion coming only from *Dicranoweisia contermina* and from *Plagiopus oederianus*. The latter is not yet known from California. The papillosity of *Amphidium* appears as bumpy ridges that run the length of the leaves and appear unrelated in placement to the placement of the cell end-walls. This pattern differs from normal papillosity that appears to arise from over the cell lumina as seen from vertical view.

Species included in this key: all Rhabdoweisiaceae, except *Grimmia* (Grimmiaceae)

Amphidium californicum (Hampe ex C. Müller Hal.) Brotherus

Amphidium lapponicum (Hedwig) W. P. Schimper

Amphidium mougeotii (Bruch & W. P. Schimper) W. P. Schimper

Grimmia anomala Hampe in W. P. Schimper

Amphidium is exclusively a moss that grows on rather shaded rock faces, crevices and protected underhangs. Typically it forms tight clumps of plants with elongate and crispate leaves. The basal cells are elongate with marginal cells somewhat more narrow than the marginal cells. There is no alar differentiation. *Amphidium* in our region is only occasionally with sporophytes but those sporophytes easily signal the identification by their sulcate and gymnostomous capsules emergent to almost immersed on a short seta.

- A. Leaf margins bistratose at mid-leaf; costa short-excurrent; immediate supra-basal marginal cells with thin lateral walls compared to the thick transverse walls. see *Dicranoweisia*
- A. Leaf margins unistratose throughout; costa ending within one or more cells of leaf apex; immediate suprabasal marginal cells without strong difference between lateral and transverse wall thickness. B
- B. Leaf margins plane or only slightly recurved at immediate base; basal cells with cuticular papillae that extend onto the stem; papillae on upper and median cells appearing as discrete bumps on the cells. *Amphidium lapponicum*
- B. Leaf margins recurved throughout the entire length of the keeled base; cuticular papillae in parallel rows. C
- C. Leaves not crispate; leaf apices with clusters of green gemmae; basal marginal cells quadrate with transverse walls thicker than lateral walls. *Grimmia anomala*
- C. Leaves strongly crispate; gemmae absent; basal marginal cells elongate with lateral and transverse walls evenly thin. D
- D. Margin serrulate with teeth so remote and irregular as to appear merely as accidental modifications; parallel papillar streaks mostly 4–6 per cell; basal juxtacostal cells primarily about 3–5:1. *Amphidium californicum*
- D. Margin entire; parallel papillar streaks mostly 3–4 per cell; basal juxtacostal cells primarily about 2–3:1. *Amphidium mougeotii*

Anacolia W. P. Schimper, 1876. *nomen conservandum*

The mosses in this key are acrocarpous mosses with narrowly subulate leaves and excurrent costae. Leaf cross-sections often show bands of multistratose laminal cells. The lower portions of the stems are always cloaked with dense red-brown, densely papillose rhizoids. These rhizoids are inserted in a halo around incipient branch buds, and the complex including the rhizoids is termed the macronematal apparatus. The macronematal apparatus is shown throughout the Order Bryales, and is probably homologous with the pseudoparaphyllial complex in pleurocarpous mosses. The shape and size of the macronematal apparatus is often of taxonomic significance, and it can easily be seen by removing leaves and most of the rhizoids from the stems. The macronematal apparatus then appears as a cluster of thin-walled, pale cells surrounded by the stumps of the removed rhizoids.

The family Bartramiaceae includes two western North American groups—the subulate-leaved *Anacolia*, *Bartramia*, *Flowersia* and *Plagiopus*, and the lanceolate leaved *Philonotis* and *Conostomum*. Axillary hairs have been found to be of special value in the Bartramiaceae (Griffin and Buck 1989) but study of that feature shows incomplete agreement with the leaf shape features. *Anacolia*, *Bartramia*, and *Plagiopus* have filamentose axillary hairs without basal brown cells while *Philonotis* has very short, distally enlarged axillary hairs with a strongly differentiated basal brown cell. *Conostomum* and the southwestern United States *Flowersia* (segregated from *Anacolia*) have elongate hairs with strongly differentiated basal brown cells.

Species included in this key: all Bartramiaceae

- Anacolia baueri* Hampe
- Anacolia laevisphaera* (Taylor) Flowers in Grout
- Anacolia menziesii* (Turner) Paris
- Bartramia halleriana* Hedwig*
- Bartramia ithyphylla* Bridel
- Bartramia pomiformis* Hedwig
- Bartramia stricta* Bridel
- Plagiopus oederianus* (Swartz) H. Crum & L. E. Anderson*

Anacolia is easily recognized even in the field by the combination of the narrowly subulate, somewhat to strongly erect leaves on a plant whose older portions are covered with richly red-brown rhizoids so dense as to obscure the stem. *Anacolia* grows on rock outcrops and on thin soil over those outcrops. It is abundant on moist outcrops but may be found even on more mesic microsites on desert fringes. Like other members of the Bartramiaceae, *Anacolia* has highly distinctive capsules, mostly spherical or short elliptic with an inconspicuously apiculate operculum. These capsules are not truly sulcate but they are strongly and irregularly wrinkled when deoperculate.

- A. Leaf base erect and encircling stem thus forming a sheath from which arises the outwardly flexed limb. *Bartramia ithyphylla*
- A. Leaf base not strictly erect, not forming a sheath. B
- B. Leaves strongly crispate when dry. C
- B. Leaves stiffly erect or spreading when dry. E
- C. Leaves three-ranked with stem cross-section rounded triangular; median laminal cells cuticular papillose. *Plagiopus oederianus**
- C. Leaves spirally inserted with stem cross-section rounded pentagonal; median laminal cells pro-rate. D
- D. Leaf base gradually contracted toward leaf limb without a definition of a shoulder; plant glaucous; capsule exerted on a long seta. *Bartramia pomiformis*
- D. Leaf base with parallel sides, constricted to the limb at a region clearly defined as a shoulder; plants brownish-green; capsule on such a short seta as to appear immersed. *Bartramia halleriana**
- E. Leaves not at all plicate at base; plant mostly growing on soil in moist to seasonally moist habitats. *Bartramia stricta*
- E. Leaves plicate at least at immediate base; plant mostly growing on rocks or on very thin soil over rocks. F
- F. Cells prorate at both their distal and proximal ends in most of limb. *Anacolia laevisphaera*
- F. Cells nearly smooth except in extreme distal portion of limb. G
- G. Capsule oblong to short-cylindric; spores less than 25 µm broad; seta more than 1 cm long; dry leaves on branch apices forming a tight cluster with all subulae closely parallel. . . *Anacolia baueri*
- G. Capsule ovoid to globose; spores more than 25 µm; seta less than 1 cm long; leaves of branch apices forming a loose cluster with all subulae lightly divergent. *Anacolia menziesii*

Andreaea Hedwig, 1801.

Andreaea is a moss that grows exclusively on acidic rocks, primarily granite. In a gametophytic state it is almost non-descript and might be interpreted as a diminutive *Didymodon* or a muticous *Grimmia*. There are three basic forms of the genus in California. The commonest expression is an ecostate and papillose form; another form is costate and smooth-celled with somewhat falcate leaves; the third form is a large snow-melt species that has costate and papillose leaves. Once encountered, *Andreaea* will be reliably recognized by the red-brown to almost black coloration of even the younger portions of the plant. This color recognition can be confirmed by close observation of the sporophytes, dehiscent not by an operculum but by longitudinal slits, a feature reminiscent of capsule dehiscence in liverworts. Our most common species of *Andreaea* may form cushions or tufts in rather moist sites; some of the other species may be far less conspicuous with the plant growing in tufts so small as to find easy camouflage among the hornblende crystals of its granite substrate.

Species included in this key: all Andreaeaceae

- Andreaea alpestris* (Thedenius) Bruch & W. P. Schimper
- Andreaea blyttii* W. P. Schimper
- Andreaea heinemannii* Hampe & C. Müller Hal.
- Andreaea nivalis* W. J. Hooker
- Andreaea rothii* Weber & D. Mohr
- Andreaea rupestris* Hedwig
- Andreaea schofieldiana* B. M. Murray

Recent work has shown spore size and morphology to be very important in *Andreaea*. Fortunately, the unique (for a moss) pattern of sporophyte maturation allows access to spores even when no exserted sporophytes can be found. Perichaetial leaves are usually larger or otherwise differentiated, and searching inside of the perichaetial leaf cluster will often yield a young but fully mature sporophyte whose pseudopodium has not yet elongated. The crushing of such a hidden sporophyte will yield spores appropriate for investigation.

- A. Leaves ecostate; perichaetial leaves convolute-sheathing, much larger than adjacent vegetative leaves. B
- A. Costa present, at least above leaf base; perichaetial leaves not strongly convolute-sheathing. . . . C
- B. Leaves somewhat secund; papillar salients on dorsal portion of mid-leaf mostly higher than leaf thickness. *Andreaea rupestris*
- B. Leaves nearly straight and symmetrical; papillar salients low to inconspicuous throughout leaf. *Andreaea alpestris*
- C. Median laminal cells sharply papillose; leaf margins crenulate to minutely serrate. *Andreaea nivalis*
- C. Median laminal cells smooth; leaf margins entire or nearly so. D
- D. Costa in extreme base of leaf only 1–3 cells thick, or not visible; plant dioicous; cells of lamina and abaxial cells of costa smooth; leaf limb moderately or not at all differentiated from the leaf base. E
- D. Costa present and not much flattened toward leaf base; plant autoicous; leaf at least somewhat constricted above an oblong-ovate base to a subulate or lanceolate limb. F
- E. At least some of the leaves bluntly rounded at apex; costa missing in extreme leaf base; median basal cells of leaf quadrate; spores mostly less than 18 μm *Andreaea heinemannii*
- E. Leaves subulate, not bluntly rounded; costa at least two cells thick to base; median basal cells of leaf rectangular with unpitted, straight lateral walls; spores mostly 25–30 μm in diameter. *Andreaea blyttii*
- F. Leaf limb more than twice as long as the leaf base; spores 35–50 μm in diameter. . . . *Andreaea rothii*
- F. Leaf limb less than twice as long as the leaf base; spores 20–30 μm in diameter. *Andreaea schofieldiana*

Anoetangium Schwägrichen, 1811. see *Gymnostomum*

Anoetangium aestivum (Hedwig) Mitten*

Anoetangium has not yet been collected in California. It is one of the rather small group of Pottiaceae with plane margined leaves and cells in the leaf rather heterogeneous in size and shape. In the field, *Anoetangium* closely resembles *Gymnostomum* except for the pattern of obscurely tristichous leaves and a more rich green coloration. When sporophytes are present they will seem to arise from the apices of

short, lateral branches. This latter character is shared with *Molendoo sendtneriana*, but *Anoectangium* has the costa confined to a narrow median groove, not present in *Molendoo*.

Anomobryum W. P. Schimper, 1860. see Pohlia

Anomobryum julaceum (Schrader ex P. G. Gärtner, B. Meyer & Scherbius) W. P. Schimper

Our one species of *Anomobryum* grows in the northern half of the state on thin soil over rocks primarily on roadcuts or cliff-bases, or along intermittent streamlets. This glossy, gray-green acrocarpous plant is readily recognized by its strongly julaceous, rather elongate stems.

Antitrichia Bridel, 1819.

The mosses here included are easily recognized by the plumose growth form. Some bryologists speak of dendroid mosses but we find it necessary to distinguish plumose mosses (erect to ascending axes from which regularly arranged branches appear in a planar fashion) from dendroid mosses (branches radiating like those of a palm tree rather than planar). We treat all our truly dendroid mosses in the key to *Neckera*.

The plants placed in this key have secondary branches that are at least somewhat julaceous. A number of plumose mosses have strongly complanate arrangement of the leaves of the secondary branches. These complanate and plumose plants are keyed under *Neckera*. Finally, the *Hylocomium* key deals with those plumose mosses that have leaves equally arranged around the stem but with those leaves or at least their portions spreading. All these mosses treated in the present section have relatively short and thick-walled median cells with the lumen: wall ratio seldom exceeding 5:1.

Species included in this key: all Leucodontaceae except *Bestia* (Brachytheciaceae); *Dendroalsia* (Cryphaeaceae); *Alsia* (Leptodontaceae); and *Pseudoleskeella* (Leskeaceae)

- Alsia californica* (W. J. Hooker & Arnott) Sullivant
- Antitrichia californica* Sullivant in Lesquereux
- Antitrichia gigantea* (Renauld & Cardot) Kindberg
- Bestia longipes* (Sullivant & Lesquereux) Brotherus
- Dendroalsia abietina* (W. J. Hooker) E. Britton in Brotherus
- Pseudoleskeella serpentinensis* P. Wilson & Norris
- Pterogonium gracile* (Hedwig) J. E. Smith

Our two species of *Antitrichia* are individually very easily recognized, but the field characters are such that they may be seen as very different plants in the field. The strongly julaceous plants of *A. californica* grow both as lithophytes and epiphytes, and are common in mesic to geographically dry areas throughout the state. The narrowly recurved leaf margins and abruptly reflexed apiculus of this large moss make recognition certain. *Antitrichia gigantea* is restricted to coastal forests of high humidity and precipitation. The red stems and spreading leaves of this very large pleurocarpous moss may suggest *Rhytidiadelphus loreus* but the latter species has closely and regularly plicate leaves while those of *Antitrichia gigantea* are irregularly wrinkled or basally lightly plicate. The costae of both species of *Antitrichia* are flattened and thus broadened near the base, and there is usually some elaboration into accessory lateral costae. *Antitrichia*, like other members of its family, has sporophytes emergent from long acicular perichaetia whose leaves are several times longer than the adjacent vegetative leaves. Such strong differentiation of the perichaetial leaves provides a character that, among California mosses, is unique to the family.

Of special interest is the bryogeography of some of these plants. The genera *Alsia* and *Dendroalsia* are endemic to west coastal North America, and there they completely replace the globally widespread *Cryphaea* and *Leucodon*. Of additional interest is the distribution of *Antitrichia* (very rare in eastern United States but found in scattered localities in Eurasia and Africa) and *Pterogonium* (absent from eastern United States but found in Eurasia and Africa).

- A. Paraphyllia present, usually densely inserted on stems and larger branches; costae single, ending above mid-leaf. B
- A. Paraphyllia absent; plants mostly julaceous; costa weak, or basally flattened and forking into subsidiary costae. C
- B. Cells strongly prorate; plant plumose and tending to curl into a ball upon drying; branch leaves conspicuously 5-ranked. *Dendroalsia abietina*
- B. Cells smooth; plant plumose or not, never strongly distorted on drying; branch leaves not conspicuously ranked. *Alsia californica*
- C. Cells strongly prorate; costa mostly ending near leaf middle, often distally forked; branches sometimes strongly attenuate with the entire branching system resembling a bird's foot. *Pterogonium gracile*

- C. Cells smooth; costa mostly stronger; branches usually not strongly attenuate. D
- D. Leaves with costa extending above the leaf middle with its distal portion of costa cloaked with dorsal spines or cristae. *Bestia longipes*
- D. Leaves with costa of various lengths but not cloaked with dorsal spines or cristae. E
- E. Leaves with costa strong and terete near base but forking distally and disappearing around mid-leaf. *Pseudoleskeella serpentinensis*
- E. Leaves with costa flattened at the base, mostly forked at that base into supplementary costae. . . F
- F. Plant julaceous; cell walls little pitted; supplementary costae less than 5 cells long.
. *Antitrichia californica*
- F. Plant not julaceous; cell walls strongly pitted throughout leaf; supplementary costae much stronger. *Antitrichia gigantea*

Aphanorrhagma* Sullivant in A. Gray, 1848. see *Acaulon

Aphanorrhagma serratum (W. J. Hooker & Wilson) Sullivant in A. Gray*

Aphanorrhagma is one example of a cluster of minute, essentially annual bryophytes that appear in winter and early spring on the open soils of grasslands and savannahs, or on the exposed soil of disturbed areas or drying pond margins. The members of this genus have the capsules immersed and nearly globose, and they arise from costate and ovate leaves with serrulate to entire margins closely inserted on a stem so short as to be inconspicuous to essentially absent. The median laminal cells are rather short-elongate, never isodiametric, and those cells are consistently smooth.

Archidium* (Hedwig) W. P. Schimper, 1826. see *Acaulon

The plants included in this section have narrowly lanceolate, often subulate leaves on a stem so short as to seem almost absent. The sporophytes are cleistocarpous and immersed on a short seta, and those sporophytes are almost spherical and contain only a few spores so huge as to be visible with the naked eye. Among the mosses of California, only *Lorentziella* has sporophytes of similar size.

Species included in this key: all Archidiaceae, except *Lorentziella* (Gigaspermaceae)

- Archidium alternifolium* (Dickson ex Hedwig) Mitten
- Archidium donnellii* Austin*
- Lorentziella imbricata* (Mitten) Brotherus

Archidium has, so far, been encountered only once in California. It is one of our smallest mosses, and it grows as a winter ephemeral (Note here that the majority of mosses considered ephemeral seem to perennate near the soil surface rather than dying back and regenerating primarily from spores). In the field, it will appear as a very small *Pleuridium*-like moss but the capsules are difficult to view because they are essentially sessile and overtopped by the leaves. We suggest that the genus is probably overlooked in the state, and will be found by careful scrutiny of sterile clones of tiny acrocarpous mosses with narrowly lanceolate to subulate leaves. Often such searching requires the combing of one's finger over the surface of the clone to reveal the capsules hidden beneath.

- A. Leaves broadly ovate, abruptly contracted into a narrow concolorous awn; sporophyte nearly sessile with a broadly elliptic capsule. *Lorentziella imbricata*
- A. Leaves lanceolate, often narrowly so; gradually contracted to the acute apex; sporophyte nearly sessile with a spherical capsule. B
- B. Median cells of larger leaves extremely variable in size and shape, often with quadrate cells adjacent to long elliptic cells; perigonia on lateral branches with fully defined bracts.
. *Archidium donnellii**
- B. Median cells of larger leaves uniformly short rectangular to rhombic; antheridia usually naked in axils of lower perichaetial leaves. *Archidium alternifolium*

Arctoa* Bruch & W. P. Schimper, 1846. see *Kiaeria

- Arctoa fulvella* (Dickson) Bruch & W. P. Schimper
- Arctoa hyperborea* (Withering) Bruch & W. P. Schimper*

Arctoa is rarely encountered on moist alpine rocks in the extreme north of California. It is one of a group of high elevation petricolous mosses that have a strong resemblance to *Dicranum*. This latter genus is absent from high elevations in California, and all our species of *Dicranum* are markedly larger than any of the members of the four higher elevation genera of comparison: *Arctoa*, *Cynodontium*, *Kiaeria*,

and *Blindia*. *Arctoa* differs from *Blindia* in lacking strong alar differentiation; unlike *Cynodontium*, *Arctoa* has smooth median laminal cells are smooth and the leaves are not markedly crispate when dry. The sporophytes of *Arctoa* are erect and symmetric; those of *Kiaeria* are inclined and asymmetric.

Atractylocarpus* Mitten, 1869. nomen conservandum. see *Campylopus

Atractylocarpus flagellaceus (C. Müller Hal.) R. S. Williams

Atractylocarpus has only recently been found in the state of California, and the species represents a major range extension from central Mexico. It is one example of the cluster of acrocarpous mosses with somewhat asymmetric leaves and with the costa filling most of the leaf base. A median leaf cross-section will clearly separate it from other such mosses. There is both a strong dorsal and ventral stereid band with a clearly defined dorsal and ventral epidermis on that costa. Unlike *Campylopus*, *Atractylocarpus* has a symmetrical and cylindric capsule on an erect seta. Our specimens grow on seepages on cliffs formed by roadcuts.

***Atrichum* Palisot de Beauvois, 1804. nomen conservandum**

In this key we treat acrocarpous mosses with photosynthetic lamellae but with those lamellae few, leaving much of the leaf lamina not covered. The plants included here are crispate and often undulate.

Species included in this key: all Polytrichaceae

- Atrichum selwynii* Austin
- Atrichum tenellum* (Röhring) Bruch & W. P. Schimper in Bruch & W. P. Schimper*
- Atrichum undulatum* (Hedwig) Palisot de Beauvois
- Bartramiopsis lescurii* (T. P. James) Kindberg*
- Oligotrichum aligerum* Mitten*
- Oligotrichum hercynicum* (Hedwig) Lamarck & A. P. de Candolle*
- Oligotrichum parallelum* (Mitten) Kindberg*

Atrichum is a very common moss of soil banks and other areas of exposed mineral soil in most of the moist, low to medium elevation areas of California. It is absolutely unmistakable even under the hand-lens. Its leaves are undulate even when moist; the strongly developed limbidium has prominent marginal teeth, mostly geminate; and the low photosynthetic lamellae, in a hand-lens view, appear as markedly darkened streaks over the costa.

The species of *Atrichum* are close and difficult to distinguish. The sexuality of individual species has been one of the more emphasized of characters in the genus. Unfortunately, we have found the dioicous character attributed to *A. selwynii* to be questionable. On several occasions plants observed in the field as male have, upon visits in later years, been found to have changed with age into female plants.

Among the more useful characters in *Atrichum* may be leaf shape, height of photosynthetic lamellae, and size and wall thickness of median laminal cells. The height of the photosynthetic lamellae is best determined by inspection of a number of excised leaves with subsequent cross-sectioning of the leaf seen under the dissection scope.

- A. Leaves with a well-defined limbidium of elongate cells and with that limbidium possessing geminate teeth. B
- A. Leaves without a limbidium and marginal teeth singly placed. E
- B. Highest photosynthetic lamellae 4–6 or more cells in height; median leaf cells 25–40 µm in longest diameter; cell walls thin with minute corner thickenings; calyptra without hairs. C
- B. Highest photosynthetic lamellae 4 or fewer cells in height; median leaf cells to 25 µm in longest diameter; cell walls thick with corner thickenings; calyptra with a few hairs on its distal portions. D
- C. Leaves comose distally, normally with a few teeth protruding off the lamina along lines of the undulations; leaves rather blunt at apex; capsule cylindric, more than 4:1, widest near its base. *Atrichum selwynii*
- C. Leaves evenly spaced along the stem, with teeth on lamina absent or few and blunt; leaves acute at apex; capsule oblong, less than 2:1. *Atrichum tenellum**
- D. Leaves evenly spaced around the stem; laminal cells above the leaf middle isodiametric; capsules arcuate, mostly less than 4 mm long. *Atrichum undulatum*
- D. Leaves comosely arranged on stem; laminal cells above the leaf middle transversely elongate; capsules nearly straight, mostly longer. *Atrichum* species A
- E. Leaf base with uniseriate, multicellular cilia on leaf shoulders; lamina at mid-leaf bistratose. *Bartramiopsis lescurii**
- E. Leaf shoulders without such cilia; lamina unistratose or with bistratose streaks. F

- F. Leaves ovate to oblong, broadest at or above the middle; leaf base not prominently sheathing; lamellae few, confined to the costa that is not distally expanded. *Oligotrichum parallelum**
- F. Leaves lanceolate from a sheathing base; lamellae more than 10, arising from a broadened costa and sometimes from the lamina. G
- G. Leaves with prominent lamellae on both the adaxial and the abaxial surfaces. *Oligotrichum aligerum**
- G. Leaves with lamellae restricted to the adaxial surface. *Oligotrichum hercynicum**

***Aulacomnium* Schwägrichen, 1804. nomen conservandum**

In this key we treat acrocarpous mosses with serrate to dentate leaves and centrally unipapillose isodiametric median leaf cells. Most specimens have clusters of multicellular gemmae at the ends of specialized gametophytic stalks (gemmaephores).

Species included in this key: all *Aulacomniaceae*

Aulacomnium androgynum (Hedwig) Schwägrichen

Aulacomnium palustre (Hedwig) Schwägrichen

Our two species of *Aulacomnium* are both very common in appropriate habitats. *Aulacomnium androgynum* is a plant of rotten or burned wood and coniferous tree bases, only occasionally petricolous; *Aulacomnium palustre* is a plant of wet and peaty soil in wetlands.

Aulacomnium androgynum almost always has "gemmaephores" (erect continuations of the main stems with terminal, globose clusters of elliptical gemmae). Such a feature, unique among local mosses, is found in both species of the genus but *A. palustre* shows the feature with less regularity. Note that the gemma cup of *Tetraphis* may be confused with the *Aulacomnium* gemmaephore, but the *Tetraphis* structure has the gemmae basally surrounded by modified leaves. One of the valuable signal characters for both species of local *Aulacomnium* in the field is the glistening, pearly-white, often distally sinuose costa.

- A. Plant mostly on rotten logs and stumps; erect, microphyllous branches with spherical, apical clusters of fusiform gemmae typically present; basal cells not at all inflated; rhizoid initials in a short-elliptical 1.5–2.5:1 cluster. *Aulacomnium androgynum*
- A. Plant mostly on soils in bogs; gemmaephores scarce with the gemmae leaf-like; basal cells of leaves more or less inflated; rhizoid initials in a longer cluster. *Aulacomnium palustre*

***Barbula* Hedwig, 1801.**

Here we include a group of acrocarpous plants with at least a trace of papillosity, and often with the papillosity obscuring the cell outlines. The leaves are typically broader than those on plants assigned to *Didymodon*, but they are more narrow than those of *Tortula* or *Syntrichia*. Unlike the latter two genera, *Barbula*, *Didymodon* and *Pseudocrossidium* technically have a trace of an adaxial stereid band on well-developed leaves but that stereid band may be elusive on many specimens.

Species included in this key: all *Pottiaceae*

Barbula convoluta Hedwig

Barbula ehrenbergii (Lorentz) Fleischer

Barbula eustegia Cardot & Thériot

Barbula orizabensis C. Müller Hal.*

Barbula unguiculata Hedwig

Bryoerythrophyllum recurvirostrum (Hedwig) C. P. Chen

Pseudocrossidium crinitum (Schultz) Zander

Pseudocrossidium obtusulum (Lindberg) H. Crum & L. E. Anderson

The several species of *Barbula*, in the sense in which we view the genus, are, in California, rather uncommon plants of disturbed or semi-desert sites. Most past treatments included in *Barbula* species that we treat under *Didymodon*. *Barbula* differs from *Didymodon* in rather technical microscopic characters: clear, rather than brown basal cells of the axillary hairs; a well-developed adaxial epidermis on the costa; and more densely papillose cells. Field differentiation can, however, rely upon the density of papillosity that results in an appearance of greater opacity in *Barbula*. Our local species of *Barbula* differ from *Didymodon* in having a smaller length:width ratio of the leaves: typical *Barbula* has elliptic to ovate or ligulate leaves while those of *Didymodon* are lanceolate, often narrowly so. The broader leaves of *Didymodon* may allow confusion with *Tortula*, and this is reflected in our treatment of *Pseudocrossidium*, a genus historically segregated from *Tortula*.

- A. Leaves with hyaline to yellowish awns; juxtalaminar, abaxial cells of the costa surface usually enlarged and yellowish-brown to orange in a pair of uniseriate rows on each side of costa.*Pseudocrossidium crinitum*
- A. Leaves without hyaline awns; juxtacostal, abaxial cells along distal portion of costa not differentiated. B
- B. Margins of leaves very strongly revolute in one or more spirals; thin walled cells with hollow papillae present within the spiralled margin; abaxial costal epidermis differentiated in cross-sectional view.*Pseudocrossidium obtusulum*
- B. Margins of leaves not so strongly revolute and differentiated; costa without a differentiated abaxial epidermis. C
- C. Leaf margins recurved almost to leaf apex; costa percurrent to shortly excurrent and mucronate. D
- C. Leaf margins recurvature restricted to base or sometimes extending nearly to leaf middle; costa various. E
- D. Leaves ovate to ovate-lanceolate, mostly less than 3:1; costa on at least some leaves mucronate in the rather blunt apex; plant green to brownish-green without any reddish blush; margin at leaf apex crenulate papillose but without any trace of toothings; median leaf cells less than 10 µm in diameter.*Barbula orizabensis**
- D. Leaves lanceolate to ligulate-lanceolate; mostly more than 4:1; costa mostly subpercurrent but not mucronate; plant usually with a reddish blush; margin of leaf apex often with enlarged cells giving a hint of toothings; median leaf cells more than 10 µm in diameter.*Bryoerythrophyllum recurvirostrum*
- E. Costa very shortly excurrent in the mucronate apex; median leaf cells so papillose as to obscure the outlines of the cell lumen; plant mostly of disturbed habitats; leaf margins recurved to near apex.*Barbula unguiculata*
- E. Costa mostly subpercurrent; median cells only lightly and inconspicuously papillose; leaf margins plane, or recurved only in proximal half. F
- F. Costa percurrent in the rounded to obtuse apex; median leaf cells nearly smooth or obscurely papillose; plant of calcareous semi-aquatic habitats often associated with tufa deposits.*Barbula ehrenbergii*
- F. Costa ending before the rounded apex; median leaf cells papillose with lobed papillae which are inserted over the central lumen and thus not obscuring the cell outlines; plant of disturbed areas especially along streams. G
- G. Perichaetial leaves, at least in part, rounded-obtuse or bluntly acute with these leaves convolute-sheathing.*Barbula convoluta*
- G. Perichaetial leaves acute with the inner ones abruptly contracted to a subulum, these leaves loosely ascending.*Barbula eustegia*

Bartramia* Hedwig, 1801. see *Anacolia

- Bartramia halleriana* Hedwig*
- Bartramia ithyphylla* Bridel
- Bartramia pomiformis* Hedwig
- Bartramia stricta* Bridel

The species of *Bartramia* exhibit a puzzling array of gross morphological features: one of our species, *B. pomiformis*, is strongly crispate; another, *B. ithyphylla*, has abruptly expanded, sheathing leaf bases; and our third species, *B. stricta*, has neither character. Despite this diversity, the three species are recognizable by the combination of very narrowly subulate leaves that appear very opaque because of the multistratose leaf lamina, along with the abundance of reddish rhizoids that obscure the stem. Like other members of the Bartramiaceae, *Bartramia* has nearly spherical capsules, wrinkled but not sulcate, very narrow mouthed but with a diplolepidous peristome. *Plagiopus*, not yet found in California, has the crispate leaves of *Bartramia pomiformis* but its obscurely tristichous leaves mark it well, even in the field.

Bartramiopsis* Kindberg, 1894. see *Atrichum

- Bartramiopsis lescurii* (T. P. James) Kindberg*

Bartramiopsis is known from only a single site in northwestern Washington State. It is easily recognized even in the field as a moderately large moss with photosynthetic lamellae and with long cilia on the shoulders of each leaf.

Bestia Brotherus in Engler & Prantl, 1906. see Antitrichia, Neckera

Bestia longipes (Sullivant & Lesquereux) Brotherus

Bestia is a monotypic genus, strictly epipetric and rather common in the San Francisco Bay area but with its abundance diminished in all directions from that area. *Bestia longipes* has blunt to obtuse leaves; short elliptic to almost isodiametric cells; a strong and abaxially cristate costa; and numerous thick-walled, isodiametric cells. Many plants have a prostrate growth pattern along with a somewhat julaceous habit, and they may thus give a gross field resemblance to *Scleropodium*; other plants may be quite dendroid to plumose and resemble an *Isothecium*. Neither of the two latter genera have short to isodiametric median laminal cells.

Blindia Bruch & W. P. Schimper 1846. see Dicranum, Kiaeria

Blindia acuta (Hedwig) Bruch & W. P. Schimper

Blindia is a strictly epipetric moss that ranges from alpine sites to near sea level, especially in the extreme north of the state. It closely resembles a *Dicranum* both in gross morphology (acrocarpous moss with smooth median cells and subulate leaves), and in microscopic features (strongly demarcated and inflated alar regions). Familiarity with the single local species of this genus involves a recognition of its small size relative to *Dicranum* as well as the silky look provided by the regularly arranged, narrowly subulate leaves. The rust-red to russet coloration of the rather glossy plants provides an additional signal character. *Blindia* is encountered on boulders in the splash zone of creeks and rivers, rock walls of waterfalls, or on rock surfaces wet by snow melt.

Brachydontium Fürnrohr, 1827. see Seligeria

Brachydontium olympicum (Britton) McIntosh & Spence*

Brachydontium trichodes (Weber) Milde*

Brachydontium with its close relative *Seligeria*, is one of the smallest acrocarpous mosses, usually becoming visible only when one looks across the edge of the rocks on which it is growing. Both species are so small that they are unlikely to be collected unless they have sporophytes.

Brachymenium Schwägrichen, 1824. see Bryum

Brachymenium exile (Dozy & Molkenboer) Bosch & Sande Lacoste*

Brachymenium systylium (C. Müller Hal.) A. Jaeger*

Brachymenium spirifolium (C. Müller Hal.) A. Jaeger*

Brachymenium is one of a group of Bryaceae that is being radically revised by Dr. John Spence. He has shown as ineffective the traditional distinction between *Bryum* (pendulous to inclined capsules) and *Brachymenium* (erect capsules). In the list above of Baja California *Brachymenium*, the first two will probably be transferred to *Bryum* and the last will be transferred to *Rosulabryum*.

Brachythecium W. P. Schimper, 1853.

The mosses keyed in this section are prostrate to laxly decumbent pleurocarps mostly of mesic sites. Gametophyte characters differ widely in degree of leaf plication, in length of the usually weak costa, in length of the usually long cells, in alar cell size and shape and in the serration of the leaf margins. Sporophytes are, however, quite distinctive in the short and arcuate capsules with apiculate opercula and reddish coloration.

Species included in this key: all Brachytheciaceae except *Leptodictyum* (Amblystegiaceae)

Brachythecium albicans (Hedwig) Bruch & W. P. Schimper

Brachythecium asperrimum (C. Müller Hal.) Sullivant

Brachythecium bolanderi (Lesquereux) A. Jaeger

Brachythecium calcareum Kindberg

Brachythecium collinum (Schleicher ex C. Müller Hal.) Bruch & W. P. Schimper

Brachythecium erythrorrhizon Bruch & W. P. Schimper

Brachythecium fendleri (Sullivant) A. Jaeger

Brachythecium frigidum (C. Müller Hal.) Bescherelle

Brachythecium holzingeri (Grout) Grout

Brachythecium hylotapetum N. Higinbotham & B. Higinbotham

Brachythecium laetum (Bridel) Bruch & W. P. Schimper*

Brachythecium leibergii Grout

- Brachythecium nelsonii* Grout
- Brachythecium occidentale* (Hampe) A. Jaeger*
- Brachythecium oedipodium* (Mitten) A. Jaeger
- Brachythecium plumosum* (Hedwig) Bruch & W. P. Schimper
- Brachythecium populeum* (Hedwig) Bruch & W. P. Schimper
- Brachythecium reflexum* (Starke in Weber & D. Mohr) Bruch & W. P. Schimper
- Brachythecium rivulare* Bruch & W. P. Schimper
- Brachythecium rutabulum* (Hedwig) Bruch & W. P. Schimper
- Brachythecium salebrosum* (Weber & D. Mohr) W. P. Schimper in Bruch & W. P. Schimper
- Brachythecium starkei* (Bridel) Bruch & W. P. Schimper
- Brachythecium velutinum* (Hedwig) Bruch & W. P. Schimper
- Brachythecium venustum* De Notaris
- Cirriphyllum cirrosum* (Schwägrichen in Schultes) Grout*
- Leptodictyum riparium* (Hedwig) Warnstorf
- Pseudoscleropodium purum* (Hedwig) Fleischer in Brotherus

Brachythecium is one of the most difficult of the genera of California mosses. The genus primarily includes plants of mesic, not inundated, sites. Species in the genus *Brachythecium* may have significant differences between the shape and cell areolation of the stem and branch leaves. *Brachythecium*, as well as the family Brachytheciaceae is being revisited by several bryologists with the work of Ignatov and Huttunen (2002) especially noteworthy for the major and well-supported changes in taxonomy. For identification it is essential to look primarily at stem leaves, and unmodified reference to leaves in this key can be understood to refer to stem leaves. Most of our species have a costa reaching only somewhat past mid-leaf, and that costa almost invariably ends in one or several abaxial spines. The leaf margin is usually somewhat toothed.

Among the features required in the study of *Brachythecium*, the pattern of plication may be especially difficult. The leaf margins of *Brachythecium* are essentially always recurved at the base, and this confers an impression of plication. A plication which defines a recurvature must extend beyond the area of recurvature in order to be considered as a plication.

Alar cells of *Brachythecium* may be rectangular or they may be almost quadrate. The latter alar pattern is confounded by the pattern of opaque versus pellucid cells. Opaque alar cells under low and medium power of a compound microscope are difficult to visualize as to the pattern of cell outline. Pellucid cells can be seen even under low power. Opaque alar cells are usually rather irregular in cell outline; pellucid one are very regularly quadrate.

Field notes should usually accompany a collection suspected of being *Brachythecium*. Main stem axes as compared with higher order branches show different degrees of prostrate versus decumbent versus nearly erect orientation, and this orientation cannot usually be known in the laboratory. Often the sexuality of the plant can be seen in the field. The presence of sporophytes emerging from the perichaetia allows one to look along the stems of the same plant for the bud-like perigonia. Laboratory examination for those same features may require floating a plant in water and spreading individual stems.

- A. Costa reaching into acumen, often nearly percurrent; seta papillose; plant autoicous. B
- A. Costa shorter, usually ending at 1/2-3/4 of the leaf length. D
- B. Apex twisted on at least some leaves; leaves cordate-deltoid, 1.5-2:1. . . . *Brachythecium starkei*
- B. Apex never twisted; leaves ovate-lanceolate, 3-5:1. C
- C. Leaves somewhat spreading and rather distantly inserted so that the stems can be seen without dissection; decurrency extending several cells down stem. *Brachythecium reflexum*
- C. Leaves more appressed and imbricate, typically obscuring the stems, almost not decurrent. *Brachythecium populeum*
- D. Leaves plicate, often with plicae defining the alar region and thus ignored but with those plicae extending more than 1/4 up the leaf. E
- D. Leaves not plicate or plicae restricted to leaf base. M
- E. Alar cells quadrate to irregular, in a large group extending more than 5 cells up the margin; branches mostly prostrate to decumbent. F
- E. Alar cells fewer, mostly rectangular, somewhat inflated and decurrent; branches erect or ascending. J
- F. Leaves contracted to a linear, nearly entire awn, when dry imbricate and homomallous. G
- F. Leaves acuminate but with that acumen neither filiform nor entire; acumen serrulate to serrate. . . . H
- G. Acumen filiform with several of its terminal cells arranged in a uniseriate fashion; alar region rather dense. *Brachythecium calcareum*
- G. Acumen narrowly linear but not uniseriate distally; alar region pellucid. *Brachythecium albicans*

- H. Alar region opaque and appearing darker than adjacent lamina. *Brachythecium laetum**
- H. Alar region pellucid with constituent cells of larger diameter than those of adjacent lamina. . . I
- I. Leaves strongly falcate-secund; decurrent with cells of the decurrency rectangular, abruptly differentiated from the quadrate cells of the alar region; leaves with acumen well-demarcated; plant dioicous. *Brachythecium erythrorrhizon*
- I. Leaves straight or only obscurely falcate; short decurrent with cells of the decurrency only gradually different from cells of the alar region; leaves mostly only gradually contracted to apex; plant autoicous. *Brachythecium salebrosum*
- J. Leaves lightly to strongly falcate, sometimes with this falcation best seen as asymmetry when detached; upper leaf margin serrulate with the teeth comprised primarily of thickening of the walls on the distal end of the cells; leaves mostly less than 2.25 mm long.
. *Brachythecium leibergii*
- J. Leaves not falcate; upper leaf margin various but with teeth not so incrassate; leaves mostly more than 2.5 mm long. K
- K. Plant sparingly branched with leaves closely appressed, concave between the plications; alar and basal cells little or not at all inflated, not extending across the leaf base; margin serrate near apex, serrulate nearly to base; plant autoicous; seta mostly smooth.
. *Brachythecium occidentale**
- K. Plants with leaves erect-spreading to loosely imbricate, not keeled along costa; alar cells inflated in the decurrent auricle; margin serrulate to serrate; plant dioicous; seta papillose. L
- L. Leaves acute to bluntly acute, mostly only lightly plicate; inflated cells; region of inflated cells often occupying a well-demarcated basal auricle and the very long decurrency; seldom with inflation of interior basal cells. *Brachythecium rivulare*
- L. Leaves acuminate with apex of some leaves laterally twisted, strongly plicate; region of inflated cells including both the decurrency and one or more rows of basal cells extending inwards to costa. *Brachythecium frigidum*
- M. Alar cells, especially within the decurrency, strongly inflated in several series. N
- M. Cells of alar and decurrency region only gradually or not at all inflated, seldom more than twice as wide as upper laminal cells. O
- N. Leaves broadly ovate to oblong-ovate, abruptly contracted to a blunt apiculus; alar region not extending to costa. *Brachythecium rivulare*
- N. Leaves deltoid-triangular, gradually contracted to a short or long acumen; alar region broad, reaching to costa. *Brachythecium nelsonii*
- O. Plant small with leaves less than 1.5 mm long; margin serrate to serrulate throughout. P
- O. Plant mostly larger; alar group poorly defined with cells short-rectangular to irregular; leaves mostly entire to low serrulate below the middle. T
- P. Leaves deeply concave with the plants somewhat julaceous; alar cells in a large group extending more than 10 cells up the margin. *Brachythecium collinum*
- P. Leaves not concave, or the plants larger. Q
- Q. Leaf cells mostly less than 6:1; plant dioicous; seta papillose throughout.
. *Brachythecium bolanderi*
- Q. Leaf cells longer; plant monoicous; seta variable. R
- R. Leaves appressed, not at all plicate; plant synoicous; seta smooth. *Brachythecium fendleri*
- R. Leaves erect-spreading to loosely ascending; plant autoicous; seta papillose. S
- S. Seta rough throughout. *Brachythecium velutinum*
- S. Seta smooth, or somewhat papillose at immediate base. *Brachythecium venustum*
- T. Leaves falcate-secund with short basal plications; alar cells short-rectangular, decurrent in a rather broad, triangular group. *Brachythecium erythrorrhizon*
- T. Leaves not falcate-secund; decurrency various. U
- U. Stem leaves deeply concave, abruptly narrowed to an apiculus or an acumen, often with the apices of some or all leaves twisted or reflexed. V
- U. Stem leaves not abruptly apiculate from a concave base; apices of leaves not twisted. X
- V. Stem and branch leaves abruptly narrowed to a very narrow acumen which is at least $\frac{1}{4}$ as long as the rest of the leaf. *Cirriphyllum cirrosum**
- V. Leaves without such a narrow acumen. W
- W. Plant strongly julaceous with branching regular and in a single plane; leaves with an abrupt short and reflexed acumen; plant restricted to lawns and similar disturbed areas.
. *Pseudoscleropodium purum*
- W. Plant neither julaceous nor with planar branching; leaves with acumen twisted; plant of medium to high elevations in the Cascades. *Brachythecium hylotapetum*

- X. Alar region poorly defined with the cells not at all inflated, quadrate to short-rectangular at least some of the plant often with a red-brown cast. Y
- X. Alar region moderately well-defined with the cells short rectangular, often somewhat inflated plants green. Z
- Y. Leaves with a well-defined acumen filled with elongate cells, ascending and somewhat hom-omallous; plant mostly mesic, on soil, logs or rocks. *Brachythecium plumosum*
- Y. Leaves acute to bluntly acute, without a defined acumen, with distal cell typical very short; leaves obliquely inserted, appearing somewhat complanate; plant aquatic or on very wet soil. *Leptodictyum riparium*
- Z. Some leaves 3–5 cells decurrent with rectangular cells; median cells mostly with straight walls. AA
- Z. Leaves less decurrent with cells of the decurrency slightly inflated; median cells vermicular. AB
- AA. Stem leaves ovate lanceolate, broadest at about ⅓; acumen long but only gradually defined; seta nearly smooth. *Brachythecium holzingeri*
- AA. Stem leaves deltoid, broadest near the base; acumen mostly rather abruptly defined; seta coarsely papillose. *Brachythecium oedipodium*
- AB. Plant dioicous; dry leaves little distorted, appearing acuminate; leaves typically with a single short plica on each side. *Brachythecium asperrimum*
- AB. Plant autoicous; dry leaves with the margins ascending and thus appearing apiculate at apex; leaves often irregularly wrinkled but not plicate even at the base. *Brachythecium rutabulum*

Braunia* Bruch & W. P. Schimper, 1846. see *Hedwigia

Braunia secunda (W. J. Hooker) Bruch & W. P. Schimper*

The occurrence of *Braunia secunda* in Arizona and in Baja California suggests the possibility of its occurrence in California. Like other members of the Hedwigiaceae, *Braunia* has papillose cells and deeply concave, ecostate leaves. Unlike *Hedwigia* and *Pseudobraunia* it lacks a hyaline awn and has some plications at the leaf base.

Breidleria* Loeske, 1910. see *Hypnum

Breidleria pratensis (Koch) Loeske*

Breidleria is a monotypic genus segregated from *Hypnum* on the basis of more conspicuous lanceolate pseudoparaphyllia, inflated alar cells, and an unusually prominent hyalodermis. *Breidleria pratensis* is not found in California but in Oregon it is an occasional plant of rocks and tree bases in swampy areas of the coastal forests.

***Bruchia* Schwägrichen, 1824.**

The plants included in this key are tiny acrocarpous mosses with narrowly acuminate to subulate leaves. They may have capsules immersed or nearly so, or the capsule may be exserted and have elongate hypophyses. Some are winter-growing ephemeral mosses of lowland grassy or barren areas; others (*Trematodon boasii* and *Bruchia bolanderi*) are summer-growing ephemerals of alpine or high montane meadows with capsules appearing late in the summer.

Species included in this key: all Bruchiaceae, except *Pleuridium* (Ditrichaceae)

- Bruchia bolanderi* Lesquereux
- Bruchia flexuosa* (Swartz ex Schwägrichen) C. Müller Hal.
- Pleuridium acuminatum* Lindberg
- Pleuridium subulatum* (Hedwig) Rabenhorst
- Trematodon boasii* W. B. Schofield

None of the species included here is likely to be collected unless one sees them with sporophytes. Gametophytic plants would most likely be interpreted as small *Ditrichum*, and these will be difficult to identify. The hyaloderm of *Archidium* differs from the stem cross-sectional features of any *Ditrichum*. The short awn of *Trematodon* is filled by the costa to a degree different from that of any *Ditrichum*. The high elevation habitat of both *Bruchia bolanderi* and *Trematodon boasii* does not overlap that of any California *Ditrichum*.

- A. Leaves with a long subulate awn completely filled by the costa. B
- A. Leaves with awn not filled by the costa. C

- B. Awn comprising less than $\frac{1}{4}$ of leaf; capsule exerted on a straight seta with the urn subtended by a long hypophysis; capsule peristomate with a well-differentiated operculum, dehiscing at maturity; calyptra cucullate; plant of alpine and subalpine sites. *Trematodon boasi*
- B. Awn relatively longer; capsule barely emergent and without a long hypophysis; capsule cleistocarpous without a peristome; calyptra mitrate; plant of low elevation grasslands. *Bruchia flexuosa*
- C. Plant of alpine and subalpine sites; leaves mostly less than 8:1; median cells of leaves mostly more than 8 μ m broad; capsule long exerted above the perichaetial leaves; hypophysis as long as the urn. *Bruchia bolanderi*
- C. Plant of low elevation grassy and barren sites; leaves subulate and longer than 8:1; median cells of leaves more narrow; capsule immersed on a somewhat curved seta; hypophysis not much differentiated. D
- D. Lamina unistratose at shoulder of upper laminal and perichaetial leaves; plants autoicous, antheridia enclosed in axillary buds. *Pleuroidium subulatum*
- D. Lamina bistratose at shoulder of upper laminal and perichaetial leaves; plants paroicous, antheridia naked in the axils of upper stem leaves. *Pleuroidium acuminatum*

Bryoerythrophyllum* Chen Pan-chieh, 1941. see *Didymodon

Bryoerythrophyllum columbianum (F. J. Hermann & E. Lawton) Zander

Bryoerythrophyllum recurvirostrum (Hedwig) Chen

Bryoerythrophyllum, with *Barbula*, *Didymodon* and *Pseudocrossidium*, forms a rather non-descript assemblage of Pottiaceous genera. The four genera have papillose and isodiametric cells in lanceolate to ovate-lanceolate, entire-margined leaves usually with recurved leaf margins. The papillosity of *Bryoerythrophyllum* is radically different from that of *Didymodon*. The former genus has hollow papillae; the latter has solid papillae. This character can be seen in a leafy stem whole-mount manipulated so that a leaf surface is seen in profile. The cell lumina of *Bryoerythrophyllum* can then be seen to enter the bases of the papillae while the papillae of *Didymodon* can be seen to be formed entirely of wall material. The costae of plants in these four genera are typically with an adaxial stereid band but that band may be reduced almost to absence. The distally dentate leaves of some specimens of *Bryoerythrophyllum*, including the local *B. recurvirostrum*, stand apart from other members of this group of four genera. Unfortunately, many of our local examples of *Bryoerythrophyllum* lack such marginal toothings, and they must be recognized by other characters. The reddish coloration of older leaves and stems of all species of *Bryoerythrophyllum* facilitates recognition by the experienced bryologist. This reddish coloration can be amplified by placing a small drop of 10% KOH on the leafy plant. Similar application of KOH to *Barbula* brings about a yellowish to greenish-yellow coloration, and *Didymodon* varies in this regard but never shows such intense coloration. In this regard, it should be noted that *Barbula* resembles *Bryoerythrophyllum* in the dense concentration of papillae that obscures the upper leaf lamina. In contrast, *Didymodon* has rather translucent leaves due to the low papillae. Our species of *Pseudocrossidium* are discussed under that genus but note the strongly revolute leaf margins of members of *Pseudocrossidium* and compare with the merely recurved margins of *Didymodon* and *Barbula*.

Bryolawtonia* Norris & Enroth, 1990. see *Neckera

Bryolawtonia vancouveriensis (Kindberg) Norris & Enroth

The only species of *Bryolawtonia* in the world occupies coastal forests as far south as Monterey County in California. It has broadly rounded costate leaves with short cells, and those leaves are quite complanately arranged. In California, the above characters are shared only with *Metaneckera* and *Porotrichum*. The strongly rugose leaves of the much larger *Metaneckera* easily distinguishes that genus. The somewhat larger *Porotrichum* has more elongate basal juxtacostal cells (seldom more than 2:1 in *Bryolawtonia*), and the broad recurvature of the trailing (postical) leaf margin in the complanate *Porotrichum* is similarly a diagnostic character.

Bryoxiphium* Mitten, 1869. see *Fissidens

Bryoxiphium norvegicum (Bridel) Mitten*

Bryoxiphium is one of the very discontinuously distributed mosses. In western North America, it is rarely encountered on siliceous rocks in northwestern Washington and in Arizona and New Mexico, as well as in scattered areas in the Cordillera Oriental of Mexico. The leaves show a steady increase in

length toward the apex of the unbranched stem, and their distichous arrangement gives an almost sword-like appearance. Thus, the common name, sword-moss, is here applied.

***Bryum* Hedwig, 1801.**

Mosses included in this section are costate and acrocarpous mosses mostly with papillose rhizoids and with rather large (more than 12 µm broad) hexagonal to rectangular, rather thin-walled cells. The pendant to horizontal capsules are mostly long cylindric and the peristome is complete or nearly so. The cells are short, seldom more than 4:1, and the costa has only an abaxial stereid band or none at all.

Species included in this key: all *Bryaceae*, except *Roellia* (Mniaceae)

- Brachymenium exile* (Dozy & Molkenboer) Bosch & Sande Lacoste*
- Brachymenium spirifolium* (C. Müller Hal.) A. Jaeger*
- Brachymenium systylium* (C. Müller Hal.) A. Jaeger*
- Bryum algovicum* Sendtner in C. Müller Hal.
- Bryum alpinum* Hudson ex Withering
- Bryum amblyodon* C. Müller Hal.
- Bryum arcticum* (R. Brown) Bruch & W. P. Schimper*
- Bryum argenteum* Hedwig
- Bryum badium* (Bridel) W. P. Schimper
- Bryum barnesii* Wood in W. P. Schimper
- Bryum bicolor* Dickson
- Bryum bimum* (Schreber) Turner
- Bryum blindii* Bruch & W. P. Schimper
- Bryum caespiticiu*m Hedwig
- Bryum calobryoides* Spence
- Bryum canariense* Bridel
- Bryum capillare* Hedwig
- Bryum cyclophyllum* (Schwägrichen) Bruch & W. P. Schimper
- Bryum elegans* Nees in Bridel
- Bryum erythroloma* (Kindberg) Syed
- Bryum flaccidum* Bridel
- Bryum gemmascens* Kindberg
- Bryum gemmiferum* R. Wilczek & Demaret
- Bryum gemmilucens* R. Wilczek & Demaret
- Bryum gemmiparum* De Notaris
- Bryum klinggraeffii* W. P. Schimper*
- Bryum knowltonii* Barnes*
- Bryum laevifilum* Syed
- Bryum lanatum* (Palisot de Beauvois) Bridel
- Bryum lisae* De Notaris
- Bryum meesioides* Kindberg in Macoun
- Bryum microerythrocarpum* C. Müller Hal. & Kindberg
- Bryum miniatum* Lesquereux
- Bryum muehlenbeckii* Bruch & W. P. Schimper
- Bryum pallens* Swartz
- Bryum pallescens* Schleicher ex Schwägrichen
- Bryum pseudotriquetrum* (Hedwig) Gaertner, Meyer & Scherbius
- Bryum pyriferum* Crundwell & Whitehouse
- Bryum radiculosum* Bridel
- Bryum rubens* Mitten
- Bryum schleicheri* Schwägrichen*
- Bryum subapiculatum* Hampe
- Bryum tenuisetum* Limpricht
- Bryum torquescens* Bruch
- Bryum turbinatum* (Hedwig) Turner
- Bryum uliginosum* (Bridel) Bruch & W. P. Schimper
- Bryum violaceum* Crundwell & Nyholm
- Bryum weigelii* Sprengel
- Plagiobryum zierii* (Hedwig) Lindberg*
- Roellia roellii* (Brotherus ex Röhl) Andrews ex H. Crum

Bryum may well be the largest genus of mosses in the world with over a thousand described species exceptionally well represented in temperate and polar portions. The genus is especially common and diverse in California. Traditionally, characters of the sporophyte of *Bryum* have been considered so important as to eclipse those of the gametophyte. Spence (1988), however, includes a very usable key to western North American species of *Bryum*, and much of the key that follows in this work is heavily indebted to Spence. The cells are mostly less than 4:1, and this differentiates local species of *Bryum* from several members of the Bryaceae centered around *Pohlia*. The Bryaceae, like the Amblystegiaceae, have recently undergone significant realignment, partly based on DNA studies. Many genera, historically placed in the Bryaceae, such as *Pohlia*, *Epipterygium* and *Roellia*, are now placed in the Mniaceae. *Leptobryum* has been transferred to the Meesiaceae.

Outside of the family Bryaceae, gametophytes of *Bryum* may most easily be confused with members of the Splachnaceae (a family not yet documented for California) and Funariaceae. Members of the former family are usually collected with sporophytes, and the long or broad hypophysis characteristic of that family should allow easy differentiation. Similarly, the Funariaceae usually are collected with sporophytes, and can be recognized by the presence of a dome-shaped operculum that has essentially no apiculus. The basic pattern of areolation of the leaves of the Bryaceae typically can be distinguished from that of the Funariaceae and the Splachnaceae. The cells of the Bryaceae vary around a rhomboidal pattern; the cells of the Splachnaceae and Funariaceae vary around a quadrate to rectangular pattern. This results in a pattern of straight rows of cells in the latter two families. The leaves of the Splachnaceae and Funariaceae are mostly broadest above the middle; those of the Bryaceae are usually broader below the middle. The Bryaceae have axillary hairs of almost equal diameter from base to apex; the Funariaceae and the Splachnaceae usually have the apical cells of greater diameter than the basal cells. Finally, there is a tendency in the Bryaceae for the leaf buttress cells to extend as a shelf-like structure after leaf excision; the Splachnaceae and Funariaceae have no such shelf-like structure after leaf excision.

Features of *Bryum* that allow identification to species include patterns of asexual reproduction. Some species of *Bryum* have multicellular, mostly spherical gemmae of specific colors shallowly buried under the substratum near the stem base. Other species of *Bryum* have multicellular, usually elliptical or filamentous, stalked structures in upper leaf axils. The coloration of the leaf base may be reddened or it may be concolorous with the rest of the leaf. Such coloration features are features of the actual leaf lamina but coloration simply of the costa base is mostly irrelevant to species distinction. All *Bryum* have somewhat narrowed cells at the immediate border. The strength of the leaf border is important in species distinction. All *Bryum* have somewhat narrowed cells at immediate border but some species have markedly more elongate and narrow cells in several parallel series, and these cells of the limbidium may even make a multistratose border.

- A. Median leaf cells at least in part more than 50 μ m broad; margin strongly differentiated. *Roellia roellii*
- A. Median leaf cells more narrow. B
- B. Leaf cells echlorophyllose in distal 1/2, the leafy plant thus appearing silvery to whitish; plant of ruderal habitats, or on thin soil over rocks. C
- B. Leaves and plant not so whitish. E
- C. Costa excurrent; plant of thin soil in frequently drying sites. *Bryum lanatum*
- C. Costa percurrent to subpercurrent; plant of various sites, often ruderal. D
- D. Plants with a reddish blush on the older portions of the stems; neck of capsule as long as urn; plant of thin soil in deep recesses of rock outcrops in alpine and subalpine areas. *Plagiobryum zierii**
- D. Plants whitish or greenish to base; neck of capsule short; plant of disturbed soil and cracks in rocks, sometimes on highly nitrogenous soil such as that below bird roosts. *Bryum argenteum*
- E. Leaves with a strong limbidium that is bistratose at least in the basal 1/3. F
- E. Leaves with limbidium strong to weak or absent, consistently unistratose. M
- F. Leaves almost orbicular but so strongly distorted when dry as to obscure that character; leaf apex bluntly obtuse with costa ending before the apex. *Bryum cyclophyllum*
- F. Leaves ovate to lanceolate with acute apices; costa mostly percurrent to excurrent. G
- G. Leaves ovate to ovate-lanceolate, decurrent with the decurrency extending to the insertion of the next leaf; distal leaf margin minutely serrulate to entire. *Bryum weigeli*
- G. Leaves not so strongly decurrent. H
- H. Most median leaf cells 25–40 μ m wide; leaves broadest near middle, about 2.5:1, not contorted when dry; plants mostly with a pinkish wash; peristome with cilia fully developed. *Bryum schleicheri**
- H. Most median leaf cells less than 30 μ m wide; leaf shape various but mostly more narrow, at

- least somewhat contorted when dry; plants variously colored; peristome with cilia absent or present. I
- I. Leaves about 2.5:1; leaf margins plane throughout; capsules turbinate, less than 2:1. *Bryum turbinatum*
- I. Leaves mostly 3:1 or greater; margins recurved at least near base; capsules more elongate. J
- J. Cells of leaf base not reddened; costae not reddened in 10% KOH; plant synoicous. *Bryum arcticum**
- J. Cells of leaf base away from the costa reddened; costa and stem very deeply reddened in KOH; plant not synoicous. K
- K. Peristome with cilia reduced or absent; spores mostly more than 25 μm in diameter. *Bryum uliginosum*
- K. Peristome with cilia fully developed; spores mostly less than 25 μm in diameter. L
- L. Some capsules in excess of 5 mm long, somewhat curved at the well-defined neck; median exothelial cells elongate, 3–4:1; spores 14–20 μm in diameter. *Bryum meesioides*
- L. Capsules mostly about 3 mm long; median exothelial cells quadrate to short rectangular; spores 20–30 μm in diameter. *Bryum pallens*
- M. Leafy stems with concave leaves closely overlapping without significant reflexing of apices, thus with an overall julaceous appearance. N
- M. Leafy stems not julaceous. P
- N. Stem heavily fluted in cross-section; leaves longer than 2 mm, heavily reddened throughout; cells of leaf base somewhat inflated. *Bryum miniatum*
- N. Stem not fluted in cross-section; leaves smaller, typically reddened only near base; cells on leaf base not inflated. O
- O. Cells of distal lamina 2–3:1, leaf apices broadly acute on distal portions of the very short stem but almost truncate or cucullate on lower portions of stem. *Bryum calobryoides*
- O. Cells of distal lamina mostly more than 4:1; leaf apices acute to acuminate, not at all cucullate. *Bryum blindii*
- P. Basal leaf cells quadrate or nearly so across the width of the leaves, obviously set off from the hexagonal to rhomboidal cells of the median and distal portions of the leaf. Q
- P. Basal leaf cells rectangular with parallel walls, gradually transiting to the hexagonal to rhomboidal cells of the median and distal portions of the leaf. AG
- Q. Rhizoids deep red-brown, sparingly papillose to almost smooth, arising from a line of nematogons arranged in a single row along abaxial line of leaf insertion. *Brachymenium systylium**
- Q. Rhizoids of various colors, strongly papillose with nematogons not arranged in a single transverse row on stem. R
- R. Costa not reaching leaf apex; leaves broadly ovate and deeply concave without a well-defined limbidium; clones easily fragmented into the constituent individual axes. *Bryum gemmascens*
- R. Plants not in all respects as above. S
- S. Plants mostly more than 1 cm high with leaves somewhat contorted distally; leaves with margins somewhat recurved. T
- S. Plants smaller with leaves closely imbricate, not contorted. U
- T. Leaves with a strong reddish coloration. *Bryum muehlenbeckii*
- T. Leaves green. *Bryum gemmiparum*
- U. Bulbils present in upper leaf axils, becoming visible by their growth that causes leaf spreading; costa percurrent; stems mostly less than 1 cm long. V
- U. Bulbils not in leaf axils but with rhizoidal tubers functioning in asexual reproduction. Z
- V. Plants with a brownish to reddish-brown spinose awn at least on the distal portions of the leaves. *Brachymenium exile**
- V. Plants with awn concolorous with rest of leaf or with the costa not excurrent. W
- W. Bulbils mostly 1–2 per upper leaf axil, usually with leaf primordia well developed, several cells wide at base. *Bryum bicolor*
- W. Bulbils 2–5 per upper leaf axil. X
- X. Bulbils small, 100–200 μm in diameter; primordia absent or difficult to define. *Bryum gemmilucens*
- X. Bulbils larger, with obvious leaf primordia on their distal portions. Y
- Y. Bulbils with leaf primordia blunt to broadly acute at apices, mostly more than 250 μm in diameter. *Bryum barnesii*
- Y. Bulbils with leaf primordia narrow and needle like, mostly less than 250 μm in diameter. *Bryum gemmiferum*
- Z. Rhizoidal tubers red to red-brown with individual cells strongly protuberant or mammillose bulging. AA

- Z. Rhizoidal tubers variously colored, smooth on surface with individual cells not bulging. AB
- AA. Limbodium well-defined at mid-leaf; rhizoidal tubers mostly more than 125 μm in diameter. *Bryum rubens*
- AA. Limbodium absent or inconspicuous; rhizoidal tubers mostly less than 100 μm in diameter. *Bryum klinggraeffii**
- AB. Rhizoidal tubers brown. AC
- AB. Rhizoidal tubers red to yellow. AD
- AC. Rhizoidal tubers mostly not spherical, often pyriform, to 75 μm in longest diameter. *Bryum pyriferum*
- AC. Rhizoidal tubers spherical, more than 125 μm in diameter; costa long excurrent. *Bryum radiculosum*
- AD. Rhizoidal tubers produced on violet rhizoids. *Bryum violaceum*
- AD. Rhizoidal tubers produced on brownish rhizoids. AE
- AE. Rhizoidal tubers yellow, less than 100 μm in diameter. *Bryum tenuisetum*
- AE. Rhizoidal tubers red to yellow, larger. AF
- AF. Many of the internal basal cells of the leaf short rectangular; rhizoidal tubers yellow or with a yellowish blush. *Bryum subapiculatum*
- AF. Basal cells of the leaf consistently quadrate; rhizoidal tubers reddish. *Bryum microerythrocarpum*
- AG. Leaves broadest above or at the middle and thus appearing obovate. AH
- AG. Leaves broadest near the base. AP
- AH. Plants with filiform gemmae present in upper leaf axils. AI
- AH. Plants without such filiform gemmae. AJ
- AI. Leaves decurrent with limbodium reaching nearly or completely to the leaf apex; costa percurrent to short excurrent; gemmae long and mostly unbranched, strictly axillary in insertion. *Bryum flaccidum*
- AI. Leaves not decurrent with limbodium mostly very weak or absent at leaf apex; costa weak, mostly ceasing before leaf apex; gemmae extensively branched, inserted in leaf axils and on leaf base. *Bryum laevifilum*
- AJ. Leaves evenly spaced, not rosulate, somewhat glaucous, laterally twisted when dry. AK
- AJ. Leaves rosulate on stems, green, erect or clockwise twisted around stem when dry. AL
- AK. Leaf lamina orbicular to broadly ovate; limbodium confluent with costa at apex; plant glaucous. *Bryum elegans*
- AK. Leaf lamina elliptical, 2.5–3.5:1; limbodium ending before leaf apex; plant glossy. *Brachymenium spirifolium**
- AL. Rosulate comas forming interrupted tufts; costa short excurrent with awn reflexed back from plane of leaf; limbodium poorly defined above the leaf middle. *Bryum canariense*
- AL. Stems usually with only a single rosulate cluster; excurrent costa not reflexed; limbodium various. AM
- AM. Leaves distinctly decurrent, mostly washed with red even distally; costa percurrent to short excurrent. *Bryum erythroloma*
- AM. Leaves not decurrent, reddened only near base; costa various. AN
- AN. Limbodium weak or absent above; margins near apex nearly entire; innovational branchlets below perichaetia with leaves broader and shorter, nearly imbricate. *Bryum gemmascens*
- AN. Limbodium strong even near leaf apex; margins near apex serrulate to serrate; innovational branchlets with leaves similar to leaves of main branches. AO
- AO. Plant synoicous or autoicous; leaves erect but contorted when dry; capsule with reddish coloration when mature. *Bryum torquescens*
- AO. Plant dioicous; leaves clockwise twisted around stem when dry; capsule mostly brown when mature. *Bryum capillare*
- AP. Leaves without a defined limbodium; costa subpercurrent, percurrent or only minutely excurrent. AQ
- AP. Leaves with limbodium obvious to near apex; costa evidently excurrent. AR
- AQ. Median leaf cells short hexagonal, more than 20 μm broad; leaf apex obtuse with costa mostly ceasing below apex. *Bryum muehlenbeckii*
- AQ. Median leaf cells linear, more than 6:1, less than 10 μm broad; leaf apex acute with costa ending at apex. *Bryum alpinum*
- AR. Leaves comosely arranged at stem apices; capsule mostly less than 2.5:1; limbodium broad with at least 5 rows of cells at leaf apex. AS
- AR. Leaves equidistantly arranged along stem; capsule mostly longer; limbodium present throughout but more narrow. AU

- AS. Leaves distally narrowly acute, gradually contracted to an excurrent costa that exceeds 0.5 mm in length. AT
- AS. Leaves with costa shorter and with the lamina not so gradually contracted. . . . *Bryum knowltonii**
- AT. Endostome and exostome fused with space between the two rows of teeth forming small chambers; capsule red. *Bryum algovicum*
- AT. Endostome and exostome not so fused; capsule yellow to orange. *Bryum amblyodon*
- AU. Leaves narrowly decurrent but with decurrency reaching nearly to base of next leaf; basal cells thick-walled with lumen: wall ratio about 4–6:1, and with these cell walls irregularly thickened to pitted. AV
- AU. Leaves not so strongly decurrent; basal cells not so strongly thick-walled, never pitted. AW
- AV. Plant synoicous. *Bryum bimum*
- AV. Plant dioicous. *Bryum pseudotriquetrum*
- AW. Leaf cells seldom more than 2.5–3:1, broadly hexagonal; limbidium broader. AX
- AW. Upper leaf cells on distal leaves at least in part long rhomboidal, 5–6:1; limbidium only 2–3 cells wide near leaf apex. AY
- AX. Endostome processes with perforations as broad as long; spores 12–16 µm in diameter. *Bryum lisae*
- AX. Endostome processes with perforations to twice as broad as long; spores 18–20 µm in diameter. *Bryum pallescens*
- AY. Leaves with spinose awn that is more than ½ as long as the leaf lamina. *Bryum badium*
- AY. Leaves with nearly smooth awn that is less than ½ as long as the leaf lamina. *Bryum caespiticium*

Buckiella* Ireland, 2001. see *Plagiothecium

Buckiella undulata (Hedwig) Ireland

The genus *Buckiella* has recently been erected (Ireland 2001) to accommodate *Plagiothecium undulatum* and a related Hawaiian species (*P. draytonii*). This new genus was moved by Ireland from the Plagiotheciaceae to the Hypnaceae on the basis of symmetric leaves with cuticular papillate cells. The decurrencies that are very prominent in *Plagiothecium* are reduced to a breadth of only 1–3 cells. The plant is easily recognized in the field by its rather lime-green appearance, and its large size combined with ecostate leaves that are strongly complanate in arrangement. Our one species is very abundant on logs and even on soil in coastal humid forests of the northwestern corner of the state.

***Buxbaumia* Hedwig, 1801.**

In this key we treat one of the most distinctive of mosses. The gametophytes, male or female, are essentially invisible to the naked eye; but the sporophytes are larger than those of most other mosses. The seta is distinctive in the high papillosity that cloaks its entire length, and this seta may be the only item visible during much of the year because of the intensity of mouse predation on the capsules. The capsules are asymmetric in a manner that suggests that an originally fat and cylindrical capsule has been pressed between the fingers in the shape of an oil lantern.

Species included in this key: all Buxbaumiaceae

- Buxbaumia aphylla* Hedwig
- Buxbaumia piperi* Best
- Buxbaumia viridis* (A. P. de Candolle) Mougeot & Nestler

Two species of *Buxbaumia* have green capsules and grow on rotten logs. *Buxbaumia piperi* is the more common of these two species, and it primarily appears in early spring. The other log species, *Buxbaumia viridis*, is rarely encountered in late summer and autumn. *Buxbaumia aphylla* has brown capsules that arise from pressed mats of organic soil, especially that occupied by the lichen genus *Cladonia* (reindeer moss).

- A. Cuticle of capsule rolling back from mouth when that capsule is deoperculate and fully dry. B
- A. Cuticle separating along a dorsal split and peeling back laterally. *Buxbaumia viridis*
- B. Capsule glossy reddish-brown when dry and recently deoperculate; plant mostly on organic soil (in this area). *Buxbaumia aphylla*
- B. Capsule green to pale yellowish-brown, not at all glossy; plant mostly on logs, common. *Buxbaumia piperi*

***Calliergon* (Sullivant in A. Gray) Kindberg, 1894.**

In this key we treat pleurocarpous, costate mosses of wetland sites. The leaves typically have inflated alar cells, and they have bluntly rounded or obtuse and apiculate apices.

Species included in this key: all Campyliaceae

- Calliergon cordifolium* (Hedwig) Kindberg*
- Calliergon giganteum* (W. P. Schimper) Kindberg*
- Pseudo-calliergon angustifolium* Hedenäs
- Pseudo-calliergon trifarium* (Weber & D. Mohr) Loeske
- Pseudo-calliergon turgescens* (T. Jensen) Loeske*
- Straminergon stramineum* (Dickson ex Bridel) Hedenäs
- Sarmentypnum sarmentosum* (Wahlenberg) Tuomikoski & T. Koponen*

The species grouped here under *Calliergon* are all plants of wetland sites, often bogs and fens. Certain few characters seldom useful in other mosses must be emphasized here. All these species are to some extent decurrent but excised leaves of *Calliergon sensu stricto* show a triangular area of decurrency on each side such that the entire leaf base appears to describe a semi-circle.

“Nematogons” are cells of a leaf with the capacity to produce rhizoids. In *Calliergon* and its relatives those nematogons are best seen on each side of the tip of the costa. These nematogons appear as empty, somewhat enlarged single cells strongly contrasting with the more opaque neighboring cells.

- A. Stem leaves with proximal one-half erect and nearly parallelling the stem but falcate and acuminate above that proximal base. *Pseudo-calliergon angustifolium*
- A. Stem leaves straight, erect to weakly spreading throughout, apiculate or rounded at apex. B
- B. Alar cells, including those of the extreme margin very thin-walled and strongly inflated; basal leaf margin broadly decurrent with that decurrency at least in part several cells wide; distal portion of leaves usually with a few nematogons. C
- B. Alar cells at least at basal margin rather thick-walled, less inflated than more interior alar cells; leaf margin narrowly or not at all decurrent; nematogons present or not. E
- C. Leaves elliptic, more than 2:1, with apex having a small apiculus; plants strongly washed with a reddish blush. *Sarmentypnum sarmentosum**
- C. Leaves broadly ovate to rounded deltoid with apex obtuse to rounded; plants green to brownish green. D
- D. Cells of alar region showing a gradual transition to the cells distal to that region; plants sparingly branched, not regularly pinnate. *Calliergon cordifolium**
- D. Cells of alar region sharply delimited from the adjacent more distal cells; plants regularly pinnate. *Calliergon giganteum**
- E. Leaves mostly more than 2:1; plants mostly with a reddish wash; most of the cells of the alar region strongly inflated and thin-walled; distal portion of leaves usually with a few nematogons. *Straminergon stramineum*
- E. Leaves nearly as broad as long, never with a reddish wash; all cells of the alar region with a significant amount of wall-thickening; nematogons not present in leaf. F
- F. Stem leaves apiculate. *Pseudo-calliergon turgescens**
- F. Stem leaves with broadly rounded apex. *Pseudo-calliergon trifarium*

Calliergonella* Loeske, 1911. see *Hypnum

Calliergonella cuspidata (Hedwig) Loeske

Our one species of *Calliergonella* is an important lawn weed in moist coastal areas of the state. Similarly, it grows in wetlands especially after disturbance. It is an ecostate pleurocarpous moss whose leaves are bluntly rounded at the apex. Especially useful in field recognition is the fusiform shape of the apical bud, a feature not so well shown by any other local bryophyte. It should be noted here that *Hypnum lindbergii* Mitten has been placed in the otherwise monotypic genus, *Calliergonella*. We are not comfortable with such a placement and continue to treat it as a *Hypnum*.

***Campylium* (Sullivant in A. Gray) Mitten, 1869.**

In this key we treat a group of pleurocarpous mosses of wetlands and stream margins. These can be costate or not, and the strongly reflexed leaves have a broadened base that abruptly narrows to a channeled and entire to serrulate acumen. The ecostate members of this genus are traditionally assigned to the

separate genus, *Campyliadelphus*, but we fail to find sufficient discontinuity between the two genera to justify separate generic placement.

Species included in this key: all Campyliaceae

- Campylium chrysophyllum* (Bridel) J. M. Lange
- Campylium hispidulum* (Bridel) Mitten
- Campylium polygamum* (W. P. Schimper) C. E. O. Jensen
- Campylium radicale* (Palisot de Beauvois) Grout*
- Campylium stellatum* (Hedwig) C. E. O. Jensen

Campylium, like most of the aquatic to semi-aquatic mosses, shows unusual variation in leaf form and placement. The length of the costa and the degree of alar group demarcation should be observed on a number of leaves preferably from different parts of the plant.

- A. Costa absent or short and double. B
- A. Costa extending to, or above leaf middle. C
- B. Plant erect to decumbent with leaves mostly more than 1.5 mm long; alar cells rectangular, markedly larger than adjacent laminal cells. *Campylium stellatum*
- B. Plant prostrate with leaves mostly less than 1 mm long; alar cells quadrate, not much enlarged compared with adjacent laminal cells. *Campylium hispidulum*
- C. Alar cells inflated; leaves loosely erect; leaf apex only gradually acuminate. *Campylium polygamum*
- C. Alar cells somewhat enlarged but not inflated; leaves squarrose to very widely spreading; leaf apex abruptly acuminate. D
- D. Alar cells subquadrate, only gradually demarcated from more distal cells; leaves closely imbricate with stem apices often somewhat hamate; median cells of leaf lamina mostly more than 10:1. *Campylium chrysophyllum*
- D. Alar cells short rectangular, rather abruptly demarcated; leaves approximate to loosely imbricate; stem apices not at all hamate; median laminal cells 4–6:1. *Campylium radicale**

Campylopodiella* Cardot, 1908. see *Campylopus

Campylopodiella stenocarpa (Wilson in Seeman) P. Müller & Frahm

Campylopodiella stenocarpa has recently been shown to be related to *Paraleucobryum* and *Brothera* on the basis of the small but chlorophyllose, somewhat stereidal cells which are scattered through the middle of the costal cross-section. This finding has forced the removal of the species from the rather similar *Atractylocarpus*. This latter genus and *Campylopodiella* are both recent additions to the California flora and are distant disjuncts from central Mexico.

***Campylopus* Bridel, 1819 [1818].**

The mosses included in this key are rather large mosses with subulate or lanceolate leaves in which at least ⅓ of the leaf base is filled by the broad and flat costa. In most species that costa is percurrent to excurrent and fills most or all of the distal subula.

Species included in this key: all Dicranaceae

- Atractylocarpus flagellaceus* (C. Müller Hal.) R. S. Williams
- Campylopodiella stenocarpa* (Wilson in Seeman) P. Müller & Frahm
- Campylopus atrovirens* De Notaris*
- Campylopus introflexus* (Hedwig) Bridel
- Campylopus pilifer* Bridel*
- Campylopus pyriformis* (F. Schultz) Bridel
- Campylopus schmidii* (C. Müller Hal.) A. Jaeger
- Campylopus subulatus* W. P. Schimper in Rabenhorst
- Dicranodontium denudatum* (Bridel) E. Britton in R. S. Williams*
- Paraleucobryum enerve* (Thedenius in C. J. Hartman) Loeske*

Median leaf cross-sections are normally required for the identification of *Campylopus* and its relatives. Of special importance in this large grouping of tropical and Southern Hemisphere mosses is the nature of the stereid bands. The stereid bands are formed of clusters of cells with walls so thick as to almost obscure the lumen. The plants here considered have some development of stereid-like cells on at least the abaxial side of the costa. Sometimes there are only groups of substereids (thick-walled cells but with

the lumen appearing to be more than a pin-prick in microscopic view). *Campylopus* may have both an abaxial and an adaxial stereid band with the two bands separated by a row of thin-walled and large "guide cells." Sometimes the abaxial stereid band is not continuous across the width of the costa but is formed of islands of stereids separated laterally by groups of more enlarged and thin-walled cells.

- A. Costa with stereid bands on both abaxial and adaxial sides, mostly with well-differentiated epidermises on both surfaces but without abaxial ridges. B
- A. Costa without a well defined adaxial stereid band; epidermises and abaxial ridges various. D
- B. Leaf base with marginal cells more narrow than those interior to the margin and therefore with little differentiation of the alar region. *Campylopodiella stenocarpa*
- B. Leaf with most of the basal marginal cells quadrate and inflated strongly defining an alar region. C
- C. Median cells of leaf linear and porose; subula occupying more than 1/2 of leaf; older leaves on stem readily caducous. *Dicranodontium denudatum**
- C. Median cells of leaf rectangular but not porose; subula shorter; leaves not caducous. *Atractylotropus flagellaceus*
- D. Costa filling nearly all of leaf with cross-section 3-cells thick and with thin-walled cells on both surfaces with the interior layer of cells smaller and deeply chlorophyllose. *Paraleucobryum enerve**
- D. Costa somewhat more narrow, without a median layer of chlorophyllose cells. E
- E. Plants with fragile shoots so that the surface of the plant is often covered with fragments of small leafy shoots; costa without stereids or with a weak and interrupted layer of abaxial stereids; leaves typically without hyaline awns. F
- E. Plants without such fragile shoots; costa with a strong and continuous layer of abaxial stereids; leaves typically with hyaline awns. G
- F. Leaves evenly contracted from base to apex; costa without stereids with the abaxial cross-section showing substereids. *Campylopus subulatus*
- F. Leaves with a broadened base that abruptly contracts into a subulate apex mostly filled with the costa; costa mostly with a band of abaxial stereids. *Campylopus pyriformis*
- G. Basal juxtacostal cells thick-walled and porose with a strong red-brown pigmentation; cells of distal portion of leaf linear and vermiculose. *Campylopus atrovirens**
- G. Basal juxtacostal cells not so differentiated; cells of distal portion of leaf mostly shorter, not vermiculose. H
- H. Costa smooth abaxially. *Campylopus schmidii*
- H. Costa ribbed on abaxial surface. I
- I. Awns on dry plants reflexed away from plant axis about 90°. *Campylopus introflexus*
- I. Awns erect even on dry plants. *Campylopus pilifer**

Campylostelium* Bruch & W. P. Schimper, 1846. see *Seligeria

Campylostelium saxicola (Weber & D. Mohr) Bruch & W. P. Schimper*

Campylostelium has not yet been found in California but its presence on granitic rock at high elevations in Washington State suggests a high possibility of its occurrence here. The very small plants grow as scattered tufts or single leafy axes exclusively on rock. It would probably not be collected except when the sporophyte is present. The very narrow and crispate leaves subtend an arcuate seta with a straight and cylindrical capsule. The plant shows its affinity with *Ptychomitrium* and with the Grimmiales in the calyptra with deep basal lobing.

***Ceratodon* Bridel, 1826.**

Here we include a single genus that has lanceolate leaves with margins recurved to near the apex and has quadrate, smooth cells tending to be arranged in longitudinal rows. One should here note the almost straight (no acumination) margins of the leaves and the remote serrulation near the apex. The dry leaves vary from very crispate to almost not at all.

Species included in this key: all Ditrichaceae

- Ceratodon purpureus* (Hedwig) Bridel
- Ceratodon stenocarpus* Bruch & W. P. Schimper

Ceratodon is one of the most widespread weedy mosses in the world, being found on every continent including Antarctica. It is especially confusing because the ovate-lanceolate to lanceolate leaves with recurved margins signal *Didymodon*. This confusion is compounded by the several ecological and mor-

phological expressions of *C. purpureus*. Even seasoned bryologists sometimes discover that a puzzling specimen is simply this weedy plant. The smooth cells of *Ceratodon* may not be the aid in identification that one might wish because *Didymodon* may have papillosity so low as to be ignored without careful observation. Our two species of *Ceratodon* have similar gametophytes, and these gametophytes have a special pattern of remote serrulation near the apex (best seen in leaves from distal portions of the stems). Observation of such a pattern of serrulations is sufficient to signal the identification. *Ceratodon* is especially easy to recognize from the strumose and sulcate, lightly curved capsule. The two species are distinguishable by seta color only when the sporophytes are fully mature. *Ceratodon* is generally abundant along road banks and other disturbed sites.

- A. Seta yellow; plant occasionally locally introduced. *Ceratodon stenocarpus*
- A. Seta red-brown; plant widespread, especially in disturbed sites. *Ceratodon purpureus*

Cirriphyllum* Grout, 1898. see *Brachythecium

Cirriphyllum cirrosum (Schwägrichen in Schultes) Grout*

Cirriphyllum is a plant of perennially wet soil primarily in riparian areas of northern Washington State. It resembles a large *Brachythecium* except for the very narrow acumen that occupies about 1/3 of the otherwise broadly ovate, lightly plicate or wrinkled leaf. We do not expect this plant to occur in California.

***Claopodium* (Lesquereux & T. P. James) Renauld & Cardot, 1893.**

Here we treat pleurocarpous mosses with somewhat elongate but papillose cells. The plants are prostrate on soil or they make mats or pendent streamers on trees.

Species included in this key: all Leskeaceae, except *Meteorium* (Meteoriaceae)

- Claopodium bolanderi* Best
- Claopodium crispifolium* (W. J. Hooker) Renauld & Cardot
- Claopodium whippleanum* (Sullivant) Renauld & Cardot
- Meteorium nigrescens* (Swartz ex Hedwig) Dozy & Molkenboer*

Claopodium is one of the few local pleurocarpous mosses whose median laminal cells are strongly papillose, a feature recognizable in the field by the opaque appearance of the golden-green plant.

The many representatives of the Leskeaceae are usually recognized by the unusual feature of strongly catenulate arrangement of the dry leaves. Hand-lens inspection of any of our three species of the genus will show the signal character of a strongly color-differentiated, whitish costa that is usually somewhat sinuose. These latter two species are very difficult reliably to distinguish in the field, but the third species (*C. whippleanum*) is readily recognized by its less pinnate growth pattern, and by its lack of hyaline awns.

- A. Leaves without hyaline awns, but sometimes with the apex very narrow and occasionally uniseriate. B
- A. Leaves with hyaline, more or less flexuose awns. C
- B. Median cells seriate-papillose; base of leaf strongly cordate-auriculate; older parts of plant mostly blackened. *Meteorium nigrescens**
- B. Median cells unipapillose; base of leaf rounded but not cordate; plant green to golden-green. ... *Claopodium whippleanum*
- C. Median cells unipapillose; hyaline awn flexed outward on moist plant. ... *Claopodium crispifolium*
- C. Median cells pluripapillose; hyaline awn flexed into the clone of a moist plant. *Claopodium bolanderi*

Climacium* Weber & D. Mohr, 1804. see *Neckera

Climacium dendroides (Hedwig) Weber & D. Mohr*

Climacium, not yet found in California, may be confused only with *Leucolepis* and *Thamnobryum*. These three unrelated genera, uniquely among California mosses have a truly dendroid habit—an erect, basally unbranched stem with radially arranged branches clustered near its apex. Such genera as *Dendroalsia*, *Alsia*, and some *Isothecium* have the contrasting “plumose” growth habit that involves a more or less planar insertion of the branches on the erect stem axes. Even under a hand-lens, *Climacium* is easily distinguished from *Thamnobryum* and *Leucolepis* by the densely paraphylliate stems, and by its

elongate cells of the distal lamina. In Oregon, *Climacium* is a plant of occasionally flooded mineral soil, especially on lake and river margins. Careful collection will show it to be stoloniferous with those stolons mostly buried and heavily rhizoidal.

Conardia* Robinson, 1976. see *Amblystegium

Conardia compacta (C. Müller Hal.) H. Robinson

Conardia compacta, has a complicated taxonomic history especially involving past placement in *Amblystegium* (Amblystegiaceae) and *Rhynchostegium* (Brachytheciaceae). Its placement in its own monotypic genus in the Campyliaceae is now moderately well-accepted. It is a small pleurocarpous moss common on calcareous rock or in alkaline desert seepages where it often makes rather dense cushions, not only on rocks but also on deciduous tree bases. Under the compound microscope, identification is made easy by the papillose rhizoids compared with the smooth rhizoids of other Amblystegiaceae-like plants. The binate teeth are a second distinguishing character on the base of some of the leaves on any clone. Binate teeth are not otherwise found in local mosses except in the very dissimilar *Philonotis*. "Binate" refers to teeth twinned in the plane of the leaf in contrast to "geminate"—teeth twinned one over the other in vertical view.

Conostomum* Swartz in Weber & D. Mohr, 1804. see *Philonotis

Conostomum tetragonum (Hedwig) Lindberg

Conostomum is easily recognized by the strongly 5-ranked leaves on a small, glaucous plant with dense red-brown rhizoids on older stems. The leaves tend to be so strongly keeled as to emphasize the pattern of leaf ranking. *Conostomum* is found on moist areas at high elevations, especially below perennial snow banks. In California, it usually grows as scattered plants among other mosses, and is recognized by its glaucous cast and strongly keeled leaves.

Coscinodon* Sprengel, 1804. see *Grimmia

Coscinodon calyptratus (W. J. Hooker in Drummond) C. E. O. Jensen ex Kindberg
Coscinodon cribrus (Hedwig) Spruce*

Coscinodon, with its sister genus *Jaffuelobryum*, has a plicate and campanulate calyptra as well as a peristome with equal thickening of the outer and inner layers. The two genera have cribrate peristome teeth which remain erect rather than flexing outward from the capsule when dry. We key *Coscinodon* in *Grimmia* because none of the gametophytic characters of *Coscinodon* would alert one to look outside of *Grimmia* for identification.

Cratoneuron* (Sullivant in A. Gray) Spruce, 1867. see *Drepanocladus

Cratoneuron filicinum (Hedwig) Spruce

Cratoneuron has traditionally included the mosses now placed in *Palustriella*. These two genera were placed together because of the presence of paraphyllia in both groups. In most specimens, these paraphyllia can be found only with careful searching. The paraphyllia of *Cratoneuron* are linear while those of *Palustriella* are lanceolate. The classification which we have here adopted places the two genera in different families based upon the differences in leaf shape and plication, as well as differences in median cell length. The species in both genera are semi-aquatic mosses, often in calcareous sites. It is abundant in alkaline seeps, springs and creeks in desert and Great Basin localities. In the field, both might be thought to be *Brachythecium* except for the much stronger and thicker costa. Even in the field, excised leaves can be seen to have much enlarged and thin-walled alar cells in large groups.

***Crossidium* Juratzka, 1882.**

Here we present a single genus of acrocarpous mosses of semiarid to arid habitats. *Crossidium* is especially common on thin soil over boulders. It often grows as linear colonies in cracks in rock outcrops. Our species all have a hyaline awn on leaves with recurved margins. Even with a hand-lens, the cushion of photosynthetic filaments can often be seen as a dark green pad in the leaf center.

Species included in this key: all Pottiaceae

Crossidium aberrans Holzinger & E. B. Bartram

Crossidium crassinerve (De Notaris) Juratzka

Crossidium seriatum H. Crum & W. C. Steere
Crossidium squamiferum (Viviani) Juratzka

Hand-lens observation of the adaxial cushion of cells will allow the observer to think of a rather limited suite of pottiaceous genera and species: *Pterygoneurum* spp. have the adaxial cushion arranged into sheets (photosynthetic lamellae) and these sheets are sufficiently separated as to be individually seen with a hand-lens; *Aloina bifrons* has adaxial photosynthetic filaments but it differs from *Crossidium* by the inflexed leaf margins; *Tortula guepinii* may have a very small adaxial cushion but its leaves are rather flat, never concave; *Tortula atrovirens* has a cushion of adaxial cells along the costa but the cells of the cushion are not arranged into filaments and the leaves never have a hyaline awn.

- A. Median leaf cells mostly papillose or mammillose; terminal cell of photosynthetic filaments nearly globose; photosynthetic filaments often so low as to be inconspicuous. B
- A. Median leaf cells smooth (ignore any papillosity that may be on cells near the leaf apex); terminal cell of filaments markedly longer than wide; photosynthetic filaments so high as to obscure almost all of the leaf lamina. C
- B. Upper leaf cells mammillose or with a single central papillae; perichaetial leaves broadest near the apex; photosynthetic filaments separate to the base. *Crossidium aberrans*
- B. Upper leaf cells papillose with several C-shaped papillae; perichaetial leaves widest near the base to near the middle; photosynthetic filaments partially fused into lamellae that may be up to 4 cells high. *Crossidium seriatum*
- C. Lumen/wall ratio of upper and median cells mostly more than 4:1, the lumen therefore obvious; leaf margin recurved to revolute from base to above the leaf middle; papillae solid on terminal cell of photosynthetic filaments. *Crossidium crassinerve*
- C. Lumen/wall ratio of upper and median cells mostly less than 1:1; the lumen therefore inconspicuous; leaf margin plane at base, sometimes recurved near leaf middle; papillae hollow on terminal cell of photosynthetic filaments. *Crossidium squamiferum*

Crumia* W. B. Schofield, 1966. see *Scouleria

Crumia latifolia (Kindberg ex Macoun) W. B. Schofield

The world's only species of *Crumia* is endemic to west coastal North America where it grows in creeks or on seepages, primarily in somewhat calcareous or alkaline regions where it is usually encrusted with salts. As a spatulate leaved and pluripapillose, acrocarpous moss, it may be reminiscent of *Syntrichia* or *Tortula*. Until sporophytes with peristomes were found, *Crumia* was placed in the affinity of the gymnostomous genus *Scopelophila*. The suggestion of relationship to *Scopelophila* was based upon possession in common of a limbidium of enlarged and thick-walled isodiametric cells. A similar pattern of marginal differentiation is also found in the genus *Scouleria* (perhaps more related to *Grimmia*). The darker colored border of the spatulate leaves is highly diagnostic in the field.

Cynodontium* Bruch & W. P. Schimper, 1856. see *Dicranella*, *Dichodontium

Cynodontium jenneri (W. P. Schimper in Howie) Stirton
Cynodontium strumulosum C. Müller Hal. & Kindberg in Macoun*
Cynodontium tenellum (Bruch & W. P. Schimper) Limpricht

Cynodontium is one of a number of plants in the Dicranaceae that the uninitiated may wish to place in the Pottiaceae. Species of this genus may have papillose cells, and those cells are often quadrate. With experience, however, the quadrate cells of the Dicranaceae are distinguishable from the isodiametric cells typical of the Pottiaceae. The shape of the lumen of an isodiametric cell of the Dicranaceae is angular, therefore almost square in dorsal view; the shape of the lumen of an isodiametric cell of the Pottiaceae is rounded, therefore almost circular. Our several species of *Cynodontium* can be quite confusing with only *C. strumulosum* showing all of the characters we associate with the genus: papillose cells, serrulate to crenulate and bistratose leaf margins, and strumose capsules. One should consider this genus for small plants with crispate leaves and nearly isodiametric cells but without sheathing leaf bases. The only California species of *Cynodontium* occupies rock outcrops at high montane or alpine elevations.

Dacryophyllum* Ireland, 2004. see *Plagiothecium

Dacryophyllum falcifolium Ireland

Dacryophyllum is a name chosen for a generically distinct new discovery by Kenneth Kellman from

Monterey and Santa Cruz counties in coastal central California. The cultriform leaves are strongly complanate and closely arranged, reminding one of the much larger neotropical Neckeraceae moss, *Isodrepanium*. The plant has complanate, non-decurrent, ecostate leaves, and the stem has no hyaloderm. It cannot be confused with any other moss.

Dendroalsia* E. Britton, 1905. see *Antitrichia

Dendroalsia abietina (W. J. Hooker) E. Britton in Brotherus

Dendroalsia is one of the most conspicuous of California mosses. It often will grow in almost pure stands on large areas of the trunks of *Quercus* spp. *Dendroalsia* is especially easy to recognize when the plant is dry—each of the branches curl downward so that the entire branched plant resembles a clinched fist with its curved fingers representing the branches.

Dendroalsia can be confused only with *Alsia*. Discussion of distinctions between the two plants appears in the paragraphs on *Alsia*.

***Dichelyma* Myrin, 1833.**

The one California species of *Dichelyma* has long, almost subulate, and falcate-secund leaves. Unlike other members of the primarily aquatic Fontinalaceae, it grows largely epiphytically on only occasionally submerged substrates. It may be so sparingly branched as to be confused with such acrocarpous, falcate and subulate leaved plants as *Dicranum*. When sporophytes are present, one will see doubly peristomate capsules with a trellis-like endostome. The sporophytes are barely emergent from greatly elongated sheathing perichaetial leaves. When capsules are absent, the lack of differentiated alar cells and the rather flat costa eliminate from consideration any *Dicranaceae* and immediately identify the plant.

Species included in this key: all Fontinalaceae

Dichelyma falcatum (Hedwig) Myrin*

Dichelyma uncinatum Mitten

The two western North American species of *Dichelyma* differ somewhat in habitat. *Dichelyma uncinatum* has been found only once in California. Originally collected by Dr. Ruprecht Düll on a short trip from his German home, it grows in large quantity on the stems of *Toxicodendron* in a frequently flooded *Acer macrophyllum* forest near Willits in Mendocino Co., California. This habitat reflects its pattern of occurrence in Oregon and Washington. *Dichelyma falcatum* is more frequently found on rocks along slowly flowing streams in Washington State. Its broader leaves may suggest *Drepanocladus sensu lato* but the tristichous nature of those leaves should allow easy identification.

- A. Leaves linear lanceolate, mostly about 10:1, keeled but not strongly conduplicate with the tristichous character thus somewhat obscure; all leaves with costa long excurrent. *Dichelyma uncinatum*
- A. Leaves lanceolate, 4–6:1, so keeled and conduplicate as to appear clearly tristichous; costa on at least some leaves in a clone percurrent to very shortly excurrent. *Dichelyma falcatum**

***Dichodontium* W. P. Schimper, 1856.**

Mosses treated in this section are acrocarpous somewhat crispate plants with the costa subpercurrent to percurrent in a somewhat blunt apex. The leaf margins of dried plants are strongly inrolled, and this inrolling causes those leaves falsely to appear very narrow. This feature makes confusing the distinctions between the narrow-leaved *D. flavescens* and the relatively broader-leaved *Dichodontium pellucidum*. The leaf margins of these two species are recurved, but those of the markedly smaller *D. olympicum* are plane. All three species of the genus have rather irregular arrangement of the teeth in the distal portion of the leaves.

Species included in this key: all Dicranaceae

Cynodontium strumulosum C. Müller Hal. & Kindberg in Macoun*

Dichodontium flavescens (Dickson) Lindberg

Dichodontium olympicum Renauld & Cardot

Dichodontium pellucidum (Hedwig) W. P. Schimper

- A. Adaxial costal surface with quadrate cells throughout; leaf margins plane; cells pluripapillose with papillar salients more than 5 µm high; plant typically in zone of melt-water in very high montane areas. *Dichodontium olympicum*

- A. Adaxial costal surface with rectangular cells in at least the distal portion of leaf; leaf margins usually recurved near the base; cells mammillose or papillose with papillar salients lower. B
- B. Leaves regularly crenulate above, seldom longer than 2 mm; plant of rocky outcrops at high elevations. *Cynodontium strumulosum**
- B. Leaves irregularly serrulate above, some more than 2 mm long; plant of riverbanks and muddy seepages at many elevations.
- C. Leaves mostly more than 4:1, contracted gradually from the broad immediate base to the acuminate apex; teeth of upper leaf margin in part composed of a complete cell. *Dichodontium flavescens*
- C. Leaves about 3–4:1, broadest a few cells above the immediate leaf base and contracted to a broadly acute or obtuse apex; teeth of upper leaf margin seldom as large as a full cell. *Dichodontium pellucidum*

***Dicranella* (C. Müller Hal.) W. P. Schimper, 1856.**

Mosses treated in this section are acrocarpous and costate mosses with the subulate leaves often falcate-secund. The majority of the species have plane to erect margins but a few are recurved. All have abaxial and adaxial stereid bands in the costa, and most have bistratose streaks and/or margins in a leaf cross-section.

Species included in this key: all Dicranaceae

- Cynodontium jenneri* (W. P. Schimper in Howie) Stirton
- Cynodontium strumulosum* C. Müller Hal. & Kindberg in Macoun*
- Cynodontium tenellum* (Bruch & W. P. Schimper) Limpricht
- Dicranella crispa* (Hedwig) W. P. Schimper
- Dicranella grevilleana* (Bridel) W. P. Schimper*
- Dicranella heteromalla* (Hedwig) W. P. Schimper
- Dicranella hilariana* (Montagne) Mitten
- Dicranella howei* Renauld & Cardot
- Dicranella pacifica* W. B. Schofield
- Dicranella palustris* (Dickson) Crundwell ex Warburg
- Dicranella rufescens* (Withering) W. P. Schimper
- Dicranella schreberiana* (Hedwig) Hilferty
- Dicranella subulata* (Hedwig) W. P. Schimper
- Dicranella varia* (Hedwig) W. P. Schimper*

Dicranella is a group of largely soil inhabiting mosses mostly in the humid northwest regions of the state. In the field the large and falcate-secund *Dicranum* of logs, tree bases and soil is easily distinguished from the markedly smaller, falcate-secund *Dicranella*. Sporophytic plants are always good to have for effective identification but gametophytes without sporophytes are usually identifiable.

- A. Leaf squarrose from a strongly sheathing base. B
- A. Leaf base not abruptly expanded and sheathing. E
- B. Leaf base only gradually contracted to the lanceolate limb; leaf apex broadly obtuse to rounded. *Dicranella palustris*
- B. Leaf base abruptly contracted to the subulate limb with the shoulders defining nearly a 45° angle relative to the costa; leaf apex narrowly obtuse to acute. C
- C. Capsule erect and sulcate; distal portion of subula 2–3 cells thick, not well-differentiated in cross-section from the costa. *Dicranella crispa*
- C. Capsule inclined, sulcate or not; distal portion of subula mostly unistratose except for the margin. D
- D. Leaves distally denticulate; many of the cells at mid-leaf more than 10 µm wide; capsules sulcate when dry. *Dicranella grevilleana**
- D. Leaves entire or nearly so to the apex; cells at mid-leaf about 5 µm wide; capsules smooth when dry. *Dicranella schreberiana*
- E. Plant crispate when dry; leaf margins recurved. F
- E. Plant not crispate; leaf margins incurved or recurved and bistratose. H
- F. Median leaf cells papillose or papillose on high mammillae; leaf margins unistratose. *Cynodontium strumulosum**
- F. Median leaf cells smooth or mammillose. G
- G. Leaf margins unistratose; perigonium with acute bracts; median leaf cells mostly more than 12 µm wide. *Cynodontium jenneri*

- G. Leaf margins bistratose; perigonium with obtuse bracts; median leaf cells mostly less than 10 μm wide. *Cynodontium tenellum*
- H. Vegetative leaves lanceolate to narrowly lanceolate, with the lamina at mid-leaf mostly more than 10 cells wide on each side of the costa; leaf margins recurved at least near the base. I
- H. Vegetative leaves subulate above the middle with the lamina mostly more narrow; leaf margins plane to incurved, mostly unistratose. L
- I. Leaves bluntly rounded or obtuse at apex with margins unistratose. *Dicranella hilariana*
- I. Leaves acute to narrowly subulate at apex with margins bistratose. J
- J. Costa broad, occupying about 1/3 of the leaf base; guide cells present on adaxial surface in costa cross-section; leaf margin only minutely recurved near the base; lateral walls of the exothecial cells somewhat sinuose, not much thicker than the transverse walls. *Dicranella howei*
- J. Costa occupying up to 1/4 of leaf base; guide cells not adaxially exposed; leaf margin recurved to mid-leaf; lateral walls of the exothecial cells nearly straight, about twice as thick as the associated transverse walls. K
- K. Upper leaves to 2 mm long; leaf cells near the apex mostly two or more times as long as broad. *Dicranella varia**
- K. Upper leaves more than 3 mm long; leaf cells near the apex mostly less than twice as long as broad. *Dicranella pacifica*
- L. Seta yellow, even when old; mouth of capsule oblique when dry and deoperculate; spores nearly smooth. *Dicranella heteromalla*
- L. Seta becoming red-brown to purple at maturity; mouth of capsule not oblique; spores finely papillose. M
- M. Capsule erect or nearly so, symmetric; annulus wanting. *Dicranella rufescens*
- M. Capsule inclined to horizontal, asymmetric; annulus well developed, of two rows of cells. *Dicranella subulata*

Dicranodontium* Bruch & W. P. Schimper in Bruch & W. P. Schimper, 1847. see *Campylopus

Dicranodontium denudatum (Bridel) E. Britton in R. S. Williams*

In the field, *Dicranodontium* would be identified as a *Dicranum* on the basis of the falcate-second leaves and large size. Further inspection would show the broad costa, and one would revise the guess to *Paraleucobryum* or *Campylopus*. Removal of a leaf would then show a somewhat auriculate leaf base and the determination as *Dicranodontium* would be secure. In the Dicranaceae, the pattern of asexual reproduction by plant fragments is quite interesting—*Orthodicranum tauricum* has regular loss of leaf apices; *Campylopus subulatus* loses stem fragments with attached leaves; *Dicranodontium denudatum* loses entire leaves. The pattern of leaf loss is so constant as to allow identification of *Dicranodontium denudatum*.

***Dicranoweisia* Lindberg ex Milde, 1869.**

Mosses included in *Dicranoweisia* have crispate leaves with entire margins and acute to acuminate apices. They make compact tufts or cushions on the substratum. The taxonomy of this genus in western North America is in dispute. We have, without strong conviction, decided to recognize at the species level two infraspecific categories of the widespread *Dicranoweisia crispula* (Hedwig) Milde. In California, we have not yet, however, been able to find typical material of *Dicranoweisia crispula*.

Species included in this key: all Seligeriaceae

- Dicranoweisia cirrata* (Hedwig) Lindberg in Milde
- Dicranoweisia contermina* Renauld & Cardot
- Dicranoweisia roellii* Kindberg in Röhl*

Our two California species of *Dicranoweisia* are easily determined simply on the basis of habitat. *D. contermina* is a plant of montane rock outcrops; *D. cirrata* is a plant of logs and coniferous tree bases at low elevations.

- A. Median and basal cells with cuticular papillosity; costa with substereids, and without clear definition of the guide cells; sporophytes immersed to slightly emergent. see *Amphidium*
- A. Cuticular papillosity absent or present as long streaks restricted to median leaf cells; costa with a strong abaxial stereid band; sporophytes exerted on a long seta. B
- B. Margins recurved near the base; cuticular papillosity lacking. C

- B. Margins plane to incurved; cuticular ridges present on median laminal cells. D
- C. Plant epiphytic and on logs and fenceposts, often at low elevations; juxtacostal, immediate supra-basal cells usually with very thick walls (lumen/wall ratio often greater than 1).
..... *Dicranoweisia cirrata*
- C. Plant on soil or rocks at high elevations; juxtacostal, supra-basal cells without such wall thickening. see *Dichodontium*
- D. Basal portions of peristome teeth striate; awn comprising about 1/2 of perichaetial leaf length; plant common in forests at mid elevations. *Dicranoweisia contermina*
- D. Peristome teeth papillose throughout; awn comprising about 1/2 of perichaetial leaf length; plant rare and local in alpine regions. *Dicranoweisia roellii**

***Dicranum* Hedwig, 1801.**

The plants included in this section are large acrocarpous mosses with strongly falcate subulate leaves and short to long median laminal cells. The alar region is a sharply demarcated zone of inflated pale to reddish-brown cells.

Species included in this key: all *Dicranaceae*, except *Blindia* (Seligeriaceae)

- Blindia acuta* (Hedwig) Bruch & W. P. Schimper
- Dicranum fragilifolium* Lindberg*
- Dicranum fuscescens* Turner
- Dicranum howellii* Renauld & Cardot
- Dicranum majus* Turner*
- Dicranum pallidisetum* Ireland*
- Dicranum polysetum* Swartz*
- Dicranum rhabdocarpum* Sullivant*
- Dicranum scoparium* Hedwig
- Dicranum spadiceum* J. E. Zetterstedt*
- Dicranum sulcatum* Kindberg in Macoun
- Dicranum undulatum* Schrader ex Bridel
- Orthodicranum tauricum* (Sapehin) Smirnova

The alar region in *Dicranum* is bistratose in all the members of the narrowly defined genus (*Orthodicranum* and *Blindia* lack such a bistratose region). The costa within the narrowly defined genus is consistently strong, often excurrent, and there are two stereid bands in at least the proximal one-half of the costa. Like other members of its family, *Dicranum* tends to have plane to incurved leaf margins, and its leaves configure themselves in either a keeled or subtubular fashion; they are never completely flat. In California, *Dicranum* is mostly restricted to the northwest quarter of the state.

Among the unusual features of taxonomic use in *Dicranum* is the nature of the distal portion of the leaf on an intact specimen. Leaves are said to be keeled or cylindric-inrolled. The two sides of the leaf lamina describe an acute angle in a keeled leaf; they together describe a semicircle in a cylindric-inrolled moss. The amount of pitting of a cell is of great importance in the distinguishing of species of *Dicranum*. Cells that are pitted are thick-walled but have areas, often near their distal or proximal ends that are significantly thinner walled.

- A. Leaf, when dry, rigidly erect, and usually with the majority of the apices broken off and functioning as propagules. B
- A. Leaf apices not caducous. C
- B. Costal cross-section with obvious guide cells but with only a single layer of cells adaxial to those guide cells; capsule erect on a straight seta. *Orthodicranum tauricum*
- B. Costal cross-section with more than one layer of cells adaxial to the guide cells, these sometimes substereidal; capsule arcuate. *Dicranum fragilifolium**
- C. Alar cells in an auriculate base (often left on stem with careless dissection); margin nearly entire; median laminal cells 6–10:1, not pitted; stereids in costa lacking. *Blindia acuta*
- C. Alar region not auriculate; margin serrulate to dentate. D
- D. Median leaf cells elongate and strongly porose; costa ridged or toothed dorsally at least near the leaf apex; leaves usually somewhat falcate. E
- D. Median leaf cells nearly isodiametric, not porose; costa not ridged on abaxial surface. J
- E. Leaf lamina strongly undulate; leaves of dry plant spreading with apex of leafy stem not hamate; margin recurved near the base. *Dicranum polysetum**
- E. Leaf lamina not, or only lightly undulate; leaves of dry plant erect with the leafy stem apex thus markedly hamate; margin plane to erect. F

- F. Abaxial surface of the costa with ridges or teeth in distal 1/3. G
- F. Abaxial surface of the costa smooth throughout. I
- G. Costa at mid-leaf with two rows of guide cells; leaves mostly about 10 mm long; leaf lamina near the apex with bistratose streaks that are often abaxially dentate. *Dicranum majus**
- G. Costa at mid-leaf with only a single row of guide cells; leaves about 5–8 mm long; leaf lamina unistratose except in alar region. H
- H. Alar region with rectangular, inflated cells throughout, only gradually transitting to the rectangular cells of the mid-leaf; costa with inconspicuous dorsal ridges. *Dicranum howellii*
- H. Alar region distally bounded by a row of quadrate, inflated cells that set off that alar region from the rectangular cells of the mid-leaf; costa with dorsal ridges partly more than one cell high. *Dicranum scoparium*
- I. Costa excurrent; cells of distal portion of leaf heteromorphic in size and shape even in a single leaf. *Dicranum spadiceum**
- I. Costa ending slightly before leaf apex; cells of distal portion of leaf rectangular and similar one to another. *Dicranum rhabdocarpum**
- J. Leaves of moist plants transversely undulate, not crispate. *Dicranum undulatum*
- J. Leaves not transversely undulate; crispate when dry. K
- K. Leaf bluntly keeled to subtubular in distal portion of leaf with the cross-section at mid-leaf describing a “U”; distal portion of costa without stereid bands; capsules yellow-green to brown; most older leaves broken toward their apices. *Dicranum pallidisetum**
- K. Leaf keeled along costa from at least the middle to near the apex with the cross-section at mid-leaf describing a “V”; distal portion of costa with stereid bands; capsules brown to reddish-brown; leaves seldom broken. L
- L. Both stereid bands of median costa about 4 cells thick; costa long excurrent; leaf base inserted on stem at 60–75° angle and then abruptly ascending and crispate; laminal cells in awn 2–3:1 and prorate with prorulae as long as the cell width. *Dicranum sulcatum*
- L. Both stereid bands of median costa about 2 cells thick; costa percurrent to short excurrent; leaf ascending throughout with base inserted at less than a 45° angle; laminal cells in awn mostly isodiametric with the prorulae smaller. *Dicranum fuscescens*

Didymodon Hedwig, 1801.

The plants treated in this section are acrocarpous mosses with lanceolate to narrowly lanceolate, entire-margined leaves with densely low papillose quadrate cells.

Species included in this key: all Pottiaceae

- Bryoerythrophyllum columbianum* (F. J. Hermann & E. Lawton) Zander
- Bryoerythrophyllum recurvirostrum* (Hedwig) Chen
- Didymodon australasiae* (W. J. Hooker & Greville) Zander
- Didymodon brachyphyllus* (Sullivant in Whipple) Zander
- Didymodon eckeliae* Zander
- Didymodon fallax* (Hedwig) Zander
- Didymodon ferrugineus* (W. P. Schimper ex Bescherele) M. O. Hill
- Didymodon insulanus* (De Notaris) M. O. Hill
- Didymodon nevadensis* Zander in Zander, Stark & Marrs-Smith*
- Didymodon nicholsonii* Culmann
- Didymodon norrisii* Zander
- Didymodon occidentalis* Zander
- Didymodon revolutus* (Cardot) R. S. Williams
- Didymodon rigidulus* Hedwig
- Didymodon tectorum* (C. Müller Hal.) K. Saito*
- Didymodon tophaceus* (Bridel) Lisa
- Didymodon umbrosus* (C. Müller Hal.) Zander
- Didymodon vinealis* (Bridel) Zander
- Pseudocrossidium obtusulum* (Lindberg) H. Crum & L. E. Anderson
- Triquetrella californica* (Lesquereux) Grout

Didymodon is one of the most widespread and abundant genera in the state of California. The differing levels of interpretation of the genus have already been discussed under the genus *Barbula*. Among the unusual features which are encountered in identification of a *Didymodon* or the similar *Bryoerythrophyllum* is the reddish coloration of some species when immersed in 10% KOH. Another unusual feature is

the shape of the cells (quadrate versus rectangular) on the adaxial surface of the costa. This feature is sometimes difficult to see because of the channeling of the apex of the leaves of many species of *Didymodon*. We enable such viewing by cutting the leaf into several fragments that can then be placed on a microscope slide with the adaxial surface facing upward. Especially important in the study of *Didymodon* is distinguishing leaves that are channeled distally. Such leaves will show a V-shaped cross-section with the angle described more than 45 degrees.

Didymodon in California is extremely diverse in morphology with the existing names seeming to be inadequate for the cataloging of that diversity. We predict a significant addition of names to the California flora with future monographic study.

- A. Leaves decurrent with decurrency extending nearly to base of next leaf. B
- A. Leaves not decurrent or with decurrency only a few cells long. C
- B. Leaves strongly 3-ranked, squarrose spreading when moist from a somewhat sheathing base; plant of shallow soil over rocks, mostly in grassy areas near the coast. ... *Triquetrella californica*
- B. Leaves spirally inserted and inconspicuously ranked, closely imbricate and ascending to erect spreading; plant of calcareous seeps. *Didymodon tophaceus*
- C. Median cells of leaf densely papillose with the papillae obscuring the cell walls at least in distal portion of leaf; adaxial cells of costa mostly quadrate, densely pluripapillose with bifid papillae. ... D
- C. Median cells of leaf low and bluntly papillose to almost smooth; abaxial cells of costa short-oblong or occasionally quadrate, often nearly smooth. F
- D. Plant conspicuously reddish with coloration obvious in the walls of the laminal cells under the compound microscope; leaf margin recurved with marginal cells not significantly less papillose than interior cells. E
- D. Plant of various colors but with red coloration not obvious in the compound microscope; leaf margin revolute in at least one complete spiral with the marginal cells low papillose to almost smooth relative to the interior cells. *Pseudocrossidium obtusulum*
- E. Basal cells of normally developed leaves quadrate or nearly so; area of differentiated interior basal cells ovate; costa short excurrent in the acute and entire apex. *Bryoerythrophyllum columbianum*
- E. Basal cells short rectangular >2:1; area of differentiated basal cells elliptical to oblong, mostly with nearly parallel lateral margins; costa subpercurrent to percurrent in the rather blunt, often dentate apex. *Bryoerythrophyllum recurvirostrum*
- F. Leaf margins crenulate-papillose in distal ½; leaves not keeled; plant fragile with leafy stems breaking from clone. *Didymodon norrisii*
- F. Leaf margins entire or, if crenulate, leaves keeled; plant not very fragile. G
- G. Adaxial surface of costa at mid-leaf with elongate rectangular (>2.5:1) cells. H
- G. Adaxial surface of costa at mid-leaf with quadrate to very short rectangular cells. I
- H. Moist leaves when detached from stem describing less than 120 degrees of arc; costa broadened at base. *Didymodon fallax*
- H. Moist leaves when detached from stem describing almost 180 degrees of arc, almost impossible to lay flat on slide without cutting into short portions; costa almost evenly tapered to apex. ... *Didymodon ferrugineus*
- I. Margins recurved nearly to apex; leaf apex sometimes obtuse. J
- I. Margins recurved only in the proximal ⅔ or less; apex more narrow. M
- J. Costa medially about 8 cells broad, often branched (spurred) in its distal portion; plant of calcareous rocks. *Didymodon revolutus*
- J. Costa mostly more narrow, not spurred; plant of more varied ecology. K
- K. Leaf apex mucronate, not at all cucullate; costa very short excurrent in the mucro; leaves deltoid to deltoid lanceolate. *Didymodon tectorum**
- K. Leaf apex obtuse to bluntly acute, cucullate to somewhat concave; costa percurrent to subpercurrent; leaves ovate to ovate-lanceolate. L
- L. Cells of adaxial costa surface bulging and with proportions deeper than wide so that that surface appears convex in hand-lens view; guide cells in more than one layer below those adaxial epidermal cells. *Didymodon nevadensis**
- L. Cells of adaxial costa not bulging; guide cells in only a single layer. ... *Didymodon brachyphyllus*
- M. Lamina on each side of costa in mid-leaf erect or nearly so, thus causing the costa to appear to occupy a medial groove; leaf apex usually with a differentiated conical apical cell. N
- M. Leaves not channeled or with only a channelling of the extreme distal portion of the leaf; leaf apex usually without a differentiated conical apical cell. R
- N. Leaf apices bistratose at least in the distal portion; these apices often regularly caducous; basal cells mostly quadrate. *Didymodon occidentalis*

- N. Leaf apices unistratose and not fragile; basal cells mostly rectangular. O
- O. Leaves evenly crenulate with margins bistratose in 1–2 rows in at least the distal ½.
..... *Didymodon eckeliae*
- O. Leaves entire throughout with marginal bistratosity appearing only in marginal patches. P
- P. Leaves narrowly lanceolate (>6:1) with the apex often terminated by a cluster of rhizoids; marginal cells of leaf base often short-rectangular; dry leaves usually somewhat crispate.
..... *Didymodon nicholsonii*
- P. Leaves lanceolate but mostly proportionately broader, without terminal rhizoids; marginal cells of leaf base rectangular; dry leaves not crispate. Q
- Q. Leaves to 2.5 mm long with the apices more or less regularly erect and not very crispate; leaf margins recurved to above the middle. *Didymodon vinealis*
- Q. Leaves longer with the apices flexuose; leaf apices strongly crispate with leaf margins recurved only in distal ½. *Didymodon insulanus*
- R. Juxtacostal basal cells not so thin-walled, mostly short-rectangular with the lumen/wall ratio often less than 6:1; leaf not distally channeled. *Didymodon rigidulus*
- R. Juxtacostal basal cells thin-walled and rectangular, often somewhat inflated, lumen/wall ratio greater than 10:1; leaf usually strongly and abruptly channeled in extreme apex. S
- S. Cortical cells of stem inflated; marginal, basal cells forming a moderately differentiated area of more narrowly rectangular cells; adaxial cells of costa usually somewhat elongate.
..... *Didymodon umbrosus*
- S. Cortical cells of stem not differentiated; basal cells without a margin of more narrow cells; adaxial cells of costa uniformly quadrate. *Didymodon australasiae*

Discelium* Bridel, 1826. see *Pohlia

Discelium nudum (Dickson) Bridel

Only one species of *Discelium* (*D. nudum*) occurs in the world. This plant is easily recognized by the extremely small, echlorophyllose and ecostate leaves of the gametophyte that arise from a persistent green protonema. The reddish seta is rigidly erect except at its extreme apex, to 2.5 cm long and rather stout. The short capsule is strongly inclined to horizontal. *Discelium* is restricted to erect and eroded banks of streams and trails very near to the ocean shore in extreme northwestern California.

***Distichium* Bruch & W. P. Schimper, 1846.**

Mosses included in this section are subulate leaved acrocarps with the leaves distichous.

Species included in this key: all Ditrichaceae

- Distichium capillaceum* (Hedwig) Bruch & W. P. Schimper
- Distichium inclinatum* (Hedwig) Bruch & W. P. Schimper

Distichium is a plant of high elevation rock crevices, but it may even be found on wet soil in alpine sites. It can be identified by the combination of subulate leaves on an erect and unbranched plant. The shiny nature of the exposed leaf bases make the distichous habit especially obvious in this genus. *Distichium capillaceum* is common on soil in riparian areas, seeps and springs especially associated with *Betula occidentalis* in eastern California.

- A. Plant evenly and uniformly distichous; capsule erect and symmetric; spores 17–20 µm; plant paroicous. *Distichium capillaceum*
- A. Plant obviously distichous but with some portions of that plant rather obscurely so; capsule inclined and asymmetric; spores 30–40 µm; plant autoicous. *Distichium inclinatum*

***Ditrichum* Hampe, 1867. nomen conservandum**

In the key that appears below we treat acrocarpous mosses mostly with narrowly subulate serrulate to denticulate leaves and rectangular laminal cells. There is no alar differentiation but instead there are several cells of the basal margin that are slightly more narrow than the more interior basal cells. Paired with this key is the key to *Dicranella*, a genus with similarly subulate and denticulate leaves and rectangular laminal cells. *Dicranella* tends to have the more lateral marginal cells larger than the more interior ones. It should be noted here that all members of the Dicranaceae and Ditrichaceae have one row of extreme marginal cells somewhat more narrow than the adjacent interior cells.

Species included in this key: all Ditrichaceae

- Ceratodon purpureus* (Hedwig) Bridel
- Ceratodon stenocarpus* Bruch & W. P. Schimper
- Ditrichum ambiguum* Best
- Ditrichum flexicaule* (Schwägrichen) Hampe*
- Ditrichum heteromallum* (Hedwig) E. Britton
- Ditrichum montanum* Leiberg
- Ditrichum pusillum* (Hedwig) Hampe
- Ditrichum schimperi* (Lesquereux) Kuntze
- Trichodon cylindricus* (Hedwig) W. P. Schimper

Among the subulate leaved acrocarpous mosses, *Ditrichum* and its close relative *Trichodon* are most easily confused with *Dicranella*. Perhaps the best characteristic of *Ditrichum* is the rather constant pattern of thickening of the transverse cell walls of the lamina cells. Among our local Ditrichaceae, this thickening is best seen in *Trichodon* whose awn therefore appears crassiserrate on the margin. All our *Ditrichum* can, however, be seen to have a small amount of such thickening mostly seen as crassiserrulation on the distal margin. This pattern of wall thickening is not seen in any of our local *Dicranella*. The sporophytes of the two genera are very different: *Ditrichum* has erect and smooth sporophytes with filiform terete peristome teeth; most species of *Dicranella* have arcuate and often sulcate sporophytes with triangular flat peristome teeth.

Ditrichum gametophytes closely resemble those of *Pleuridium* in leaf shape and in having distal crasiserrulation of the leaf marginal cells. *Pleuridium*, seldom collected except with sporophytes, resembles *D. montanum* and *D. schimperi* in that the larger vegetative and perichaetial leaves have a rather well demarcated leaf base relative to the leaf limb. Furthermore, the two aforementioned *Ditrichum* differ from *Pleuridium* in having a fairly broad costa filling more than ¼ of the leaf base.

- A. Leaf margins recurved and usually bistratose (if unistratose, the vegetative leaves ovate to lanceolate, not at all subulate). B
- A. Leaf margins plane to incurved. E
- B. Median cells quadrate and isodiametric; leaves evenly contracted to the narrowly acute apex so that the line depicting the leaf margin is almost straight; peristome teeth 16, triangular. C
- B. Median cells rectangular, at least 2:1; leaves contracted above the base into a distinctive acumen. D
- C. Seta yellow; plant occasionally locally introduced, usually on roofs of buildings and on road pavement. *Ceratodon stenocarpus*
- C. Seta red-brown; plant widespread, especially in disturbed sites. *Ceratodon purpureus*
- D. Leaves of dry plant curved to crispate; peristome teeth spinose-papillose; seta red; operculum long-rostrate, usually over ½ as long as the urn. *Ditrichum ambiguum*
- D. Leaves of dry plant straight and erect; peristome teeth low-papillose to striate; seta brown to yellowish brown; operculum short-rostrate. *Ditrichum pusillum*
- E. Leaf squarrose from an abruptly expanded and strongly sheathing base; awn dorsally prorate. *Trichodon cylindricus*
- E. Leaf base not abruptly expanded and sheathing. F
- F. Median leaf cells mostly about 2:1. G
- F. Median leaf cells mostly more than 4:1. H
- G. Plant of seepages in montane calcareous springs; stems mostly exceeding 5 cm long, densely matted below with rhizoids; leaf lamina mostly unistratose or with bistratosity near apex. *Ditrichum flexicaule**
- G. Plant of moist soil, often on roadbanks; plant smaller not matted with rhizoids; leaf lamina and margins bistratose or with bistratose streaks in the upper one-half. *Ditrichum montanum*
- H. Costa very broad, filling about ⅓–¼ of leaf base; plant autoicous; spores rough, 20–29 μm. *Ditrichum schimperi*
- H. Costa more narrow; plant dioicous; spores smooth and smaller. *Ditrichum heteromallum*

***Drepanocladus* (C. Müller Hal.) G. Roth, 1899.**

Mosses treated in this section are costate pleurocarps of wetland habitats. They have smooth, elongate cells and their leaf apices are acute to acuminate. Most have enlarged alar cells, and some have those cells extending all the way to the costa.

Species included in this key: all Campyliaceae except *Cratoneuron* (Cratoneuraceae); *Leptodictyum* (Amblystegiaceae) and *Palustriella* (Helodiaceae)

Campylium polygamum (W. P. Schimper) C. E. O. Jensen
Cratoneuron filicinum (Hedwig) Spruce
Drepanocladus aduncus (Hedwig) Warnstorf
Drepanocladus capillifolius (Warnstorf) Warnstorf
Drepanocladus crassicosatus Janssens*
Drepanocladus polycarpus (Blandow ex Voit) Warnstorf
Drepanocladus sordidus (C. Müller Hal.) Hedenäs in W. R. Buck
Hamatocaulis vernicosus (Mitten) Hedenäs
Leptodictyum humile (Palisot de Beauvois) Ochyra
Leptodictyum riparium (Hedwig) Warnstorf
Palustriella commutata (Bridel) Ochyra
Palustriella falcata (Bridel) Hedenäs*
Sanionia uncinata (Hedwig) Loeske
Warnstorfia exannulata (Bruch & W. P. Schimper) Loeske
Warnstorfia fluitans (Hedwig) Loeske

All of the plants in this section have traditionally been considered a part of a family Amblystegiaceae, a family more recently split by such workers as Ochyra and Hedenäs. With the exception of *Palustriella* and *Cratoneuron*, the mosses included here were traditionally placed together in a large genus, *Drepanocladus*. *Palustriella* and *Cratoneuron* were treated separately under the larger genus, *Cratoneuron*. The reason for the separation of *Cratoneuron* derived from the presence of paraphyllia but those paraphyllia are often scarce and difficult to find.

- | | |
|---|------------------------------------|
| A. Leaves longitudinally plicate, mostly falcate-secund. | B |
| A. Leaves of wet or dry plant not plicate or, if so, not falcate. | E |
| B. Alar cells very thin-walled and hyaline in a strongly demarcated region that extends to the costa; foliose paraphyllia scattered over the stem (especially visible near the stem apex); at least the basal cells with distal prorations. | C |
| B. Alar cells not inflated and hyaline, or with the inflated cells in a smaller group; paraphyllia not present; none of the cells prorate. | D |
| C. Stem leaves deltoid-triangular with a somewhat cordate base, abruptly narrowed near the leaf middle into a long acumen; alar cells forming a large group in the cordate base. | |
| | <i>Palustriella commutata</i> |
| C. Stem leaves lanceolate and falcate, gradually narrowed from near the base to the long acuminate apex; alar cells forming a small group to 5 cells long at margin. | <i>Palustriella falcata</i> * |
| D. Stem cross-section with an obvious hyaloderm; leaves falcate-secund from the base; plant never with a reddish pigmentation, autoicous. | <i>Sanionia uncinata</i> |
| D. Hyalodermis absent; leaves straight in proximal ½, becoming falcate distally; plant mostly with a reddish pigmentation, dioicous. | <i>Hamatocaulis vernicosus</i> |
| E. Alar cells inflated and extending nearly or completely across the leaf base; plant aquatic or in seepages. | F |
| E. Alar cells not in such a large group; habitat various. | K |
| F. Plant typically brownish-green to purple or reddish; leaves with nematogons on each side of the costa, these nematogons appearing as empty cells strongly differentiated from the highly pigmented adjacent cells; plant mostly in running water of small streams. | <i>Warnstorfia exannulata</i> |
| F. Plant typically green to glaucous-green although sometimes darker due to a covering of sediments, never reddish or purple; plant without nematogons on the leaves; mostly in seepages and slow-flowing to stagnant waters. | G |
| G. Leaf margin serrate to serrulate; leaves broadly ovate, about 2:1; lanceolate to filamentous paraphyllia normally sparse but present on well-developed stems; plants of calcareous seepages. | <i>Cratoneuron filicinum</i> |
| G. Leaf margin absolutely entire, even at apex; leaves ovate-lanceolate, more than 3:1; paraphyllia absent; plant of slow-flowing or stagnant waters. | H |
| H. Costa percurrent to excurrent. | <i>Drepanocladus capillifolius</i> |
| H. Costa ending somewhat before the apex. | I |
| I. Plant with quadrate or very short rectangular cells in 1–4 rows immediately above the alar region. | <i>Drepanocladus polycarpus</i> |
| I. Alar region not set off by rows of short cells. | J |

- J. Leaves typically falcate-secund with acumen not well-demarcated from the rest of the leaf. *Drepanocladus aduncus*
- J. Leaves straight with acumen well-demarcated. *Campylium polygamum*
- K. Terminal cell of leaf 1.5–3:1; alar cells only gradually differentiated from adjacent laminal cells. L
- K. Terminal cell of leaf longer and not much differentiated; alar cells abruptly differentiated from adjacent laminal cells. M
- L. Plant mostly growing submerged in water or on frequently submerged objects; leaves obliquely attached to stem; median leaf cells mostly more than 10:1. *Leptodictyum riparium*
- L. Plants growing on mesic or very wet habitats, seldom submerged; line of leaf insertion at a right angle to the long axis of the stem; median leaf cells seldom more than 8:1. *Leptodictyum humile*
- M. Alar cells only gradually differentiated; costa of stem leaves mostly occupying more than ¼ of leaf base, bulging on both surfaces of the leaf. *Drepanocladus crassicosatus**
- M. Alar cells well-demarcated from other basal cells; costa more narrow, bulging abaxially if at all. N
- N. Alar cells thick-walled; leaf margins entire, incurved in distal portions of leaf; leaf without nematogons. *Drepanocladus sordidus*
- N. Alar cells thin-walled and inflated; leaf margins serrulate, often minutely so; nematogons present as clear cells near costa in distal portion of leaf. *Warnstorfia fluitans*

Encalypta Hedwig, 1801.

Encalypta is a genus primarily occupying areas of thin soil over rock outcrops, sometimes calcareous, sometimes siliceous. With the exception of *E. procera*, members of the genus usually have sporophytes and they are immediately recognizable by the campanulate calyptrae which completely ensheath the capsule and the upper portion of the seta. Without sporophytes, *Encalypta* is easily confused with *Syntrichia* except that most of its species have plane-margined, rather than recurved, leaves. Under the compound microscope, the pigmented lateral walls of the basal cells of *Encalypta* provide a good gametophytic character. In the field, experienced bryologists can easily recognize sterile specimens of *Encalypta*. The feature of recognition is, however, subjectively understood, and thus difficult to communicate. Basically, we look for an undulate-crispate appearance of the dry plant—a feature not duplicated in any species of *Syntrichia*.

Species included in this key: all Encalyptaceae

- Encalypta affinis* R. A. Hedwig in Weber & D. Mohr*
- Encalypta brevicollis* (Bruch & W. P. Schimper) Ångström*
- Encalypta brevipes* Schljakov*
- Encalypta ciliata* Hedwig
- Encalypta intermedia* Juratzka
- Encalypta procera* Bruch
- Encalypta rhaptocarpa* Schwägrichen
- Encalypta vulgaris* Hedwig

Traditionally, species of *Encalypta* are distinguished primarily by features of the calyptra, the peristome and the spores. These features are ordinarily useful because the sporophytes are so regularly present. Many features of the gametophyte are confusingly inconstant. A special problem is the infraspecific variation in the hyaline awn—present or absent, long or short. Perhaps the most useful diagnostic gametophytic characters of the genus are the features of basal cell coloration; shape of the line between the basal and median cells; and rhizoid size, branching pattern, and coloration.

- A. Leaf bases with very large diameter (ca. 100 µm) rhizoids inserted on abaxial costa; leaf axils densely beset with a dense cushion of rhizoids, usually gemmiparous; basal leaf cells thin-walled but trigonous, abruptly demarcated from the heavily papillose median laminal cells. *Encalypta procera*
- A. Leaf bases without such large diameter rhizoids; leaf axils without rhizoid cushions; basal leaf cells not so abruptly demarcated from median laminal cells. B
- B. Abaxial surface of basal cells papillose with that papillosity extending across the leaf or confined to a few rows of cells on the leaf margin. *Encalypta affinis**
- B. Basal cells not at all papillose or with the papillae of the median cells somewhat transgressing onto the adjacent basal cells. C
- C. Transverse walls of basal cells strongly reddened with the line between the cells of the base and those of the limb rather abrupt and almost perpendicular to long axis of leaf; calyptra not fringed. *Encalypta rhaptocarpa*

- C. Transverse walls of basal cells yellow to orange with the line between the basal and limb cells an upside-down "U"; calyptra fringed. D
- D. Leaves with a strongly developed hair point mostly more than 1.5 mm long; leaf apices mostly cucullate. E
- D. Leaves muticous or with an apiculus or short hairpoint less than 0.5 mm long. G
- E. Leaf margins recurved on both sides of proximal one-half of leaf. *Encalypta ciliata*
- E. Leaf margins plane or recurved near base on only one side. F
- F. Capsules smooth and cylindrical even when dry; calyptra with beak constituting about 1/3 of its total length. *Encalypta brevicollis**
- F. Capsules ribbed at least near mouth, often wrinkled throughout; calyptra with beak ill-defined and constituting less than 1/4 of its length. *Encalypta brevipes**
- G. Rhizoids pale and repeatedly branched, not monopodial, forming a dense cushion in leaf axils, mostly 10–12 µm in diameter; enlarged basal cells mostly 2–3:1, to 12 µm broad; seta short with capsule barely exserted above the perichaetial leaves. *Encalypta intermedia*
- G. Rhizoids red-brown, to 35 µm in diameter, monopodially branched with branches of much smaller diameter, not densely clustered in leaf axils; enlarged basal cells mostly 3–6:1, to 18 µm broad; seta longer with capsule above even the tips of the perichaetial leaves. *Encalypta vulgaris*

***Entosthodon* Schwägrichen, 1823.**

Entosthodon, like other members of the Order Funariales, is strongly reminiscent of some members of the Bryaceae. This resemblance is shown by the common possession of large and thin-walled cells, the tendency of many members to have a somewhat developed limbidium, and the basically comose growth pattern also exhibited by some members of the genus *Bryum*. Despite this basic resemblance, the two families are classified into different orders on strong phylogenetic and morphologic bases. Perhaps the most diagnostic of features of the Funariales is the endostome position. All other groups of doubly peristomate mosses except the Funariales have the endostome insertion alternate with the exostome insertion. Thus, a view of the outer surface of the peristome of a Bryalean moss under the compound microscope will show the endostome segments peeking out from between the peristome teeth. It is difficult to see the endostome in a similar view of the peristome of a Funarialean moss because each endostome segment will be positioned precisely behind each exostome tooth. Another unusual feature of most Funariales is the nature of the stomates in the capsule walls. Typical stomates are formed by a longitudinal division of the guard cell primordium to make two kidney-bean shaped guard cells that define an opening between them. In most Funariales, the last division is incomplete such that the opening is defined but the guard cells are not completely separate, and thus they together form a single donut-shaped cell.

There are subtle gametophytic differences between the Funariales and Bryales in gametophytic features. The cells of both are large and thin-walled but the basic form of the Funariales median laminal cell is rectangular while that of the Bryales is elongate-hexagonal. The rhizoids of most Bryales are papillose; those of most Funariales are smooth.

Species included in this key: all Funariaceae

- Entosthodon attenuatus* (Dickson) Bryhn
- Entosthodon bolanderi* Lesquereux
- Entosthodon californicus* (Sullivant & Lesquereux) H. Crum & L. E. Anderson
- Entosthodon drummondii* Sullivant in Sullivant & Lesquereux
- Entosthodon fascicularis* (Hedwig) C. Müller Hal.*
- Entosthodon kochii* H. Crum & L. E. Anderson
- Entosthodon planoconvexus* (E. B. Bartram) Grout*
- Entosthodon rubrisetus* (E. B. Bartram) Grout
- Entosthodon tucsoni* (E. B. Bartram) Grout

Among the Funariales, *Entosthodon* is the genus with exserted, erect and symmetric capsules with the endostome reduced and the exostome present. It is in general smaller than either *Funaria* or *Physcomitrium* but there is much overlap in size between the genera.

- A. Leaves broadly acute to obtuse. B
- A. Leaves mucronate to acuminate. C
- B. Peristome double; leaves ovate to elliptic ovate; suboral exothecial cells long and narrow, to 6 times as wide as long in up to 8 rows. *Entosthodon californicus*
- B. Exostome present and well-developed, to 250 µm long, endostome absent; leaves ligulate; suboral exothecial cells short rectangular, to 3 times as wide as long in only a few rows. *Entosthodon kochii*

- C. Costa broad and long, ending at least in the base of the acumen; capsules pyriform, less than 2:1. *Entosthodon drummondii*
- C. Costa not so extended. D
- D. Costa ending at 1/2-3/4 of leaf; leaf apex slenderly and abruptly acuminate. E
- D. Costa stronger; leaf apex various. F
- E. Exostome long and well-developed with teeth of newly deoperculate capsule meeting at their tips in the open capsule mouth; capsules pyriform, more than twice as long as wide; spores 28-30 µm in diameter; endostome present. *Entosthodon bolanderi*
- E. Exostome abortive, consisting of only a few cell fragments; capsules short pyriform to oblong, less than twice as long as wide; spores 35-40 µm in diameter; endostome absent. *Entosthodon tucsoni*
- F. Leaves nearly entire or finely crenulate, bordered by several rows of narrower cells. *Entosthodon attenuatus*
- F. Leaves with at least some serrulations near the apex, elimbate. G
- G. Capsules somewhat inclined and asymmetric; terminal cells in leaf acumen markedly elongated with only one or 2 tiers of cells in that acumen; suboral cells of exothecium not or hardly differentiated. *Entosthodon rubrisetus*
- G. Capsules strictly erect and symmetric; terminal cells of acumen not so elongate; suboral cells differentiated in 2-4 rows, transversely elongated. H
- H. Operculum flat, without an apiculus; spores mostly about 20 µm in diameter. *Entosthodon planoconvexus**
- H. Operculum with a small apiculus; spores 25-30 µm in largest diameter. *Entosthodon fascicularis**

Ephemerum* Hampe, 1837. see *Acaulon

Ephemerum serratum (Schrader ex Hedwig) Hampe

Ephemerum is probably the smallest moss in California. Throughout low elevations of the state, it can regularly be found from December to late March on eroded mineral soil and even on the trampled soil of paths and playgrounds. The plant will not be likely to be collected except with sporophytes and, even then, hand-lens viewing often yields only a suspicion that it might be there. *Ephemerum* is best recognized in the field by the densely placed cushion of erect or matted protonemata resembling strands of a green alga. These protonemata may rise more than 1 mm off the soil surface, and they may therefore obscure the narrow, almost strap-shaped leaves. It may be appropriate here to mention that moss protonemata are separable from green algal filaments on the basis that the cross-walls in the filaments of a moss protonema are oblique to the long axis but they are transverse in a green alga.

Epipterygium* Lindberg, 1862. see *Pohlia

Epipterygium tozeri (Greville) Lindberg

Our one species of *Epipterygium* is very easily recognized in the field but the compaction of the specimens in an herbarium packet may cause some confusion. This plant is common in rather humic montane and coastal sites where it grows in rather strongly shaded niches in soil bank especially along trails, road banks and creek banks. It has the metallic gloss of a *Pohlia* but the plants do not grow rigidly erect. Instead the central axis of this acrocarpous plant angles upward from the substratum with a resulting difference between a dorsal and a ventral side. The centrally placed leaves on the dorsal side of the stem are markedly more narrow and shorter than the leaves to either side. Thus, *Epipterygium* maximizes the effective photosynthetic surface by its leaf placement.

Eucladium* Bruch & W. P. Schimper, 1846. see *Gymnostomum

Eucladium verticillatum (Hedwig in Bridel) Bruch & W. P. Schimper

Our one species of *Eucladium* can easily be recognized. The strongly papillose leaves typical of the Pottiaceae are obvious even in the field by the opaque appearance of the leaves. The plane-margined leaves place *Eucladium* in an unusual place in a family dominated by recurved margined leaves. Even under a hand-lens the glaucous leaves and rather long stems suggest identification, and the observation of crenulate margins even of the upper leaves causes one to look for the rather large, often binate teeth on the leaf margin at the intersection of the rectangular and pellucid basal cells with the quadrate and pluripapillose cells of the limb. *Eucladium*, especially in the arid interior of the state, is common along seeps and springs with high calcareous or alkaline content. It is often found in areas of tufa precipitation.

***Eurhynchium* Bruch & W. P. Schimper in Bruch & W. P. Schimper, 1854.**

In the key that appears below we have included pleurocarpous mosses with costate leaves. Except for *Steerecleus*, the plants in this key have elongate median cells but drastically shorter cells of the distal portion of each leaf.

Species included in this key: all *Brachytheciaceae*

- Eurhynchium hians* (Hedwig) Sande Lacoste
- Eurhynchium pulchellum* (Hedwig) Jennings
- Eurhynchium striatum* (Schreber *ex* Hedwig) W. P. Schimper
- Kindbergia oregana* (Sullivant) Ochyra
- Kindbergia praelonga* (Hedwig) Ochyra
- Platyhypnidium riparioides* (Hedwig) Dixon
- Scleropodium colpophyllum* (Sullivant) Grout
- Steerecleus serrulatus* (Hedwig) H. Robinson

The genus *Eurhynchium* is basically a *Brachythecium* with a long rostrate operculum. We must remember that early muscologists saw the sporophyte as the moss analog of the flower and fruit of a flowering plant. The excessive importance of the sporophyte in mosses is being tempered by modern taxonomic treatments, and we are attempting to assimilate the major taxonomic reapportionments in Ignatov and Huttunen (2003). This work will surely enforce readjustment of the taxonomies in our present work, but the changes are so numerous and significant as to require a period of fermentation prior to adoption.

There are only a few gametophytic features allowing recognition of *Eurhynchium* and its allies. *Kindbergia* is a poorly differentiated genus recognizable by the squarrose stem leaves that are radically broadened relative to the more narrow and patent branch leaves, however, our two species of *Kindbergia* are easily recognized due to their branching pattern and leaf arrangement. *Platyhypnidium* is similarly a poorly differentiated genus recognizable by the almost cordate leaves on this aquatic moss. *Steerecleus* is a third segregate from *Eurhynchium* primarily distinguished by the complanate growth habit.

- A. Plants regularly pinnate, often bi- or tri-pinnate; leaf margin decurrent. B
- A. Plants irregularly, often sparingly branched; leaf decurrency short and often inconspicuous. . . . D
- B. Leaves of stems only gradually larger than those of branches, not squarrose; leafy stems mostly prostrate. *Eurhynchium striatum*
- B. Leaves of stems radically and abruptly larger, broader and more decurrent than those of branches; leafy stems usually arching above the substrate. C
- C. Plant regularly plumose with a single main stem from which arises shorter, nearly unbranched, lateral stems; plant mainly of coastal moderately low elevation sites. *Kindbergia oregana*
- C. Plant irregularly branched or tri- to tetra-pinnate; plant mainly of higher elevation, or of deeply shaded sites. *Kindbergia praelonga*
- D. Plant complanate-foliate; leaves with a well-demarcated and laterally twisted acumen and with the cells in that acumen mostly more than 4:1. *Steerecleus serrulatus*
- D. Plants not complanate; leaves not acuminate or with the acumen poorly defined; cells in acumen various but often very short. E
- E. Leaves orbicular; leaf apices not at all acuminate, plant aquatic. *Platyhypnidium riparioides*
- E. Leaves longer than broad; leaf apices blunt to obtuse; plant on mesic to rather dry sites. F
- F. Leaves deeply concave with basal cells rectangular across the entire base. *Scleropodium colpophyllum*
- F. Leaves not deeply concave; differentiated cells of leaf base confined to alar region. G
- G. Leaves ovate-lanceolate with a short but blunt acumen; seta smooth. *Eurhynchium pulchellum*
- G. Leaves elliptic to elliptic lanceolate with a broadly acute to almost obtuse apex; seta papillose throughout. *Eurhynchium hians*

***Fabronia* Raddi, 1808.**

Mosses included in this section are very small pleurocarps with elongate, thin-walled cells and with leaf margins dentate to ciliate.

Species included in this key: all *Fabroniaceae*

- Fabronia ciliaris* (Bridel) Bridel
- Fabronia pusilla* Raddi

Fabronia is one of our smallest pleurocarpous mosses. It grows on tree trunks and on rock outcrops

in filtered light throughout much of the state. If one sees a very small prostrate and branched moss on such a substratum, one should look for the very long terminal cell of each leaf. Often additional cells are similarly elongate into ciliate marginal cells but the single apical cell will define the plant. *Fabronia* has a rather silvery sheen upon close observation with a hand-lens. When growing among other mosses, *Fabronia* may be visible only when the goblet-shaped capsules emerge above associated plants.

- A. Leaves dentate with the individual teeth composed of 0.75–2.0 cells. *Fabronia ciliaris*
- A. Leaves ciliate-dentate with the teeth composed of one or more very much elongate cells.
..... *Fabronia pusilla*

***Fissidens* Hedwig, 1801.**

In the key that appears below are all the local mosses with the leaves inserted in two ranks. One should note here the frequency of “complanate mosses”—plants that appear flattened despite a spiral insertion of the leaves. Carefully observe the leaves at their lines of insertion on the stems. All complanate mosses have leaves inserted on the dorsal portion of the flattened stem and only subsequently twisted into the dominant plane.

Species included in this key: all Fissidentaceae, except *Bryoxiphium* (Bryoxiphiaceae), *Distichium* (Districhaceae) and *Schistostega* (Schistostegaceae)

- Bryoxiphium norvegicum* (Bridel) Mitten*
- Distichium capillaceum* (Hedwig) Bruch & W. P. Schimper
- Distichium inclinatum* (Hedwig) Bruch & W. P. Schimper
- Fissidens adianthoides* Hedwig
- F. aphelotaxifolius* Pursell
- F. asplenioides* Hedwig*
- F. bryoides* Hedwig
- F. crispus* Montagne
- F. curvatus* Hornschuch
- F. dubius* Palisot de Beauvois
- F. fontanus* (Bachelot de la Pylaie) Steudel
- F. grandifrons* Bridel
- F. minutulus* Sullivant
- F. osmundioides* Hedwig*
- F. pauperculus* M. A. Howe
- F. sublimbatus* Grout
- F. taxifolius* Hedwig
- F. taylorii* C. Müller Hal.
- F. ventricosus* Lesquereux
- Schistostega pennata* (Hedwig) Weber & D. Mohr*

Fissidens is one of the easiest mosses to identify to genus but, with perhaps 600 species worldwide, it may be exceptionally difficult to identify to species. We are indebted to Dr. Ronald Pursell for our understanding of the genus *Fissidens*. All species of *Fissidens* have “equitant leaves,” a feature involving an apparent splitting of the basal region so that the two sides of the split clasp the stem in the manner of the base of an *Iris* leaf. The clasping base is the “vaginant lamina.” Distal to the vaginant lamina is the “distal lamina,” and, derived from a single abaxial ridge on the costa is the “dorsal lamina.” *Fissidens* varies in size from some of the smallest of our more or less acrocarpous mosses to some that may even reach 15 mm high. Our species of *Fissidens* include large plants of flooded rocks, often in rapidly flowing streams as well as on wet rock walls of streams and seeps, and our smaller species grow primarily on disturbed soil.

- A. Leaves ampliate clasping with the antical base carinate and pocketing the stem allowing the definition of a “vaginant lamina” differentiated from the more distal, non-carinate “apical lamina” and the costal ridge which serves as a “dorsal lamina.” B
- A. Leaves deeply carinate but without differentiation into a dorsal and an apical lamina thus the plant not identifiable to *Fissidens*. Q
- B. Leaves with a strong border of elongate cells on all laminae. C
- B. Leaves not bordered, or bordered on vaginant laminae or with a group of lighter cells on dorsal and apical laminae. H
- C. Plant of submerged rocks in flowing streams; leaves more than 2 mm long; lamina and margin with bistratose streaks. *Fissidens ventricosus*

- C. Plant usually on soil; leaves smaller; lamina consistently unistratose. D
- D. Leaves narrowly attenuate with the dorsal lamina ending above the leaf base; laminal cells 2–4:1; sterile plants consistently larger and with more clearly distichous leaves than the archegoniate ones. *Fissidens curvatus*
- D. Leaves not strongly attenuate; dorsal lamina extending to or near the leaf base; laminal cells nearly isodiametric; sterile and archegoniate plants not strongly differentiated. E
- E. Cells of the lamina about as broad as thick in cross-section, mostly not very bulging; dorsal lamina extending downward and inserted on the stem; plants of rather moist habitats. *Fissidens bryoides*
- E. Cells of the lamina markedly thicker than broad in cross-section, mostly bulging mammillose; dorsal lamina mostly not extending downward to leaf insertion; plants of moist or dry habitats. F
- F. Dorsal lamina tapering to extinction at leaf insertion; plant of soils in dry grasslands. *Fissidens sublimbatus*
- F. Dorsal lamina continuing to leaf insertion; plant of moist sites mostly in western California. G
- G. Limbidium ending more than two cells below leaf apex; base of stem strongly reddened; plant usually on rocks. *Fissidens minutulus*
- G. Limbidium confluent with costa at apex; base of stem not reddened; plant usually on soil. *Fissidens crispus*
- H. Leaves with a rigid, multistratose lamina, 3–5 mm long; plant aquatic to semiaquatic especially in calcareous regions. *Fissidens grandifrons*
- H. Lamina unistratose and smaller. I
- I. Leaves flaccid, blackening when dry, mostly more than ten times as long as wide, with the vaginant lamina less than $\frac{1}{2}$ leaf length; plant immersed or seasonally immersed in streams and ponds, often calcareous. *Fissidens fontanus*
- I. Leaves neither flaccid nor so long; plant not aquatic. J
- J. Leaves serrate in distal one-half. K
- J. Leaves crenulate to entire. L
- K. Median leaf cells to 12 μm in longest dimension; leaf lamina unistratose throughout. *Fissidens adianthoides*
- K. Median leaf cells smaller; lamina at mid and upper leaf with bistratose streaks. *Fissidens dubius*
- L. Vaginant lamina with a somewhat defined limbidium; dorsal and apical laminae with markedly smaller cells on margin even to near the apex; costa percurrent; fertile plants markedly smaller than sterile plants. *Fissidens taylorii*
- L. Vaginant lamina elimbate; dorsal and apical laminae mostly not bordered or with marginal cells both smaller and paler than immediate interior cells; costa various; fertile and sterile plants of similar size and development. M
- M. Costa excurrent to percurrent on at least some of the leaves of the plant. N
- M. Costa ending below the leaf apex. O
- N. Median leaf cells smooth to slightly bulging, almost pellucid in dorsal microscopic view; leafy plants mostly less than 2 cm long; leaf apex excluding apiculus acute. *Fissidens aphelotaxifolius*
- N. Median leaf cells strongly mammillose-bulging, opaque in dorsal microscopic view; leafy plants mostly more than 2.5 cm long; leaf apex excluding apiculus obtuse to rounded. *Fissidens taxifolius*
- O. Plant less than 5 mm tall; marginal cells of leaf smaller and paler than immediate interior cells. *Fissidens pauperculus*
- O. Plant mostly more than 10 mm tall; marginal cells not so differentiated. P
- P. Median leaf cells less than 10 μm in longest dimension; leaves crenulate throughout. *Fissidens asplenioides**
- P. Median leaf cells more than 12 μm in longest dimension; leaves with at least a few serrulations near apex but crenulate below. *Fissidens osmundioides**
- Q. Leaf without any keeling, arranged flat in vertical rows; leaves confluent with one another by means of a decurrent postical base that is continuous with the antical base of the next leaf below thus resembling the leaflet arrangement of the fern *Osmunda*. *Schistostega pennata**
- Q. Leaves base carinate and pocketing the stem; leaves not confluent with one another on the stem. R
- R. At least the proximal portion of the stem with bluntly rounded leaves, without a subula; distal portion of fertile stems with long but erect subulae. *Bryoxiphium norvegicum**
- R. All the fully developed leaves with a defined, glossy base and with a divergent subulate apex. S
- S. Plant evenly and uniformly distichous; capsule erect and symmetric; spores 17–20 μm ; plant paroicous. *Distichium capillaceum*
- S. Plant obviously distichous but with some portions of that plant rather obscurely so; capsule inclined and asymmetric; spores 30–40 μm ; plant autoicous. *Distichium inclinatum*

Fontinalis Hedwig, 1801.

Mosses treated in this section are aquatic to semi-aquatic ecostate mosses with tristichous leaves that are mostly deeply keeled along mid-line.

Species included in this key: all Fontinalaceae

- Fontinalis antipyretica Hedwig
- Fontinalis chrysophylla Cardot
- Fontinalis gigantea Sullivant
- Fontinalis howellii Renauld & Cardot
- Fontinalis hypnoides C. J. Hartman
- Fontinalis mollis C. Müller Hal.
- Fontinalis neomexicana Sullivant & Lesquereux

The Fontinalaceae is a family of primarily aquatic habitats. Some species can be found in the quiet waters of ponds, and other species occupy the waters of very rapidly flowing rivers and streams. All species of *Fontinalis* have strongly tristichous leaves, and most of those species have the leaves strongly longitudinally folded along the mid-line. Often the leaves are so strongly folded that the two halves are pressed one side against the other. This latter condition of “carinate leaves” may cause the worker to see the leaf as flat and not-folded, thus interpreting the leaf shape on the basis of the shape of the longitudinally-halved leaf. Effective work on *Fontinalis* requires the unfolding of the two leaf halves with the placement of that unfolded leaf for viewing under the microscope. Very important, also, is the viewing of the intact plant to see the outline of the keel. A straight keel describes a straight line from the insertion on the stem all the way to the leaf apex. Alternatively, the keel can be curved from base to apex, or it can have a basal curve giving way to a straight distal portion. *Fontinalis*, with a maximum length of about 1 meter, is the largest moss in the state.

- C. Leaves not keeled, completely plane and very flaccid. Fontinalis hypnoides
- C. Leaves clearly carinate. D
- D. Branch apices spinulose with tightly overlapping immature leaves making a bud-like structure 5–10 times as long as its width at mid-point, triangular in cross-section; perichaetial leaves abruptly apiculate. Fontinalis neomexicana
- D. Branch apices not so strongly resolved into a bud-like structure; perichaetial leaves obtuse. . . . E
- E. Leaf, when viewed from the side, showing a nearly straight keel that basally curves abruptly to the point of insertion. F
- E. Leaf keel curved throughout. G
- F. Leaves (when spread flat) mostly about as broad as long; best-developed leaves at least 5 mm broad. Fontinalis gigantea
- F. Leaves typically nearly twice as long as broad; best-developed leaves less than 5 mm broad. . . Fontinalis antipyretica
- G. Leaves concave to nearly plane in distal portion. Fontinalis chrysophylla
- G. Leaves keeled to within a few cells of the apex. H
- H. Leaves of larger stems broadest near its middle. Fontinalis mollis
- H. Leaves broadest immediately above its base. Fontinalis howellii

Funaria Hedwig, 1801.

Members of the Funariaceae grow primarily in open soil of disturbed and desert areas. The family includes many ephemeral plants generally thought to be annuals overwintering by spores. Some of these ephemeral Funariaceae have essentially no seta, and so the capsule is immersed. Such plants are keyed elsewhere in this work.

Species included in this key: all Funariaceae

- Funaria calvescens Schwägrichen
- Funaria hygrometrica Hedwig
- Funaria microstoma Bruch ex W. P. Schimper
- Funaria muhlenbergii Turner
- Pyramidula tetragona (Bridel) Bridel

The Funariaceae are strongly reminiscent of the genus *Bryum* but the peristome is highly diagnostic. *Funaria*, as a member of the Funariales, has the endostome segments arranged opposite the exostome teeth. A side view of such a capsule may have those exostome teeth so covering the endostome segments as to render the latter invisible. In contrast, most mosses with a double peristome have the exostome

alternating in placement with the more interior endostome segments. Such an arrangement means that the endostome segments are seen between the exostome teeth when seen in a side view of the capsule.

Additional characters allowing recognition of members of this family include the usually comose arrangement of the leaves; the dome-shaped (no apiculus) operculum; and the ring-like single cell that replaces the guard cells on the stomata of the exothecial wall. Because so many of our Funariaceae are presumably annual plants, the sporophyte is usually present at the time of collection. For this reason, most of the species and generic differentia are sporophytic. *Funaria hygrometrica* is among the most widespread mosses in California. It is common on a wide variety of sites and habitats, and especially abundant on recently burned landscapes. The orange seta and mature capsules allow identification at a distance of many meters.

- A. Upper exothecial cells elongate and so strongly thickened as to appear virtually without a lumen; annulus not well-defined; spores with high papillae. *Funaria muhlenbergii*
- A. Upper exothecial cells irregularly isodiametric to irregularly oblong; annulus well-defined and revoluble; spores nearly smooth. B
- B. Upper leaves rather abruptly acuminate; endostome segments less than ½ the length of the exostome; spores mostly more than 25 µm. C
- B. Upper leaves acute to short acuminate; endostome segments almost as long as the exostome; spores mostly less than 15 µm. D
- C. Seta very short with capsule hardly exserted; calyptra plicate with four ribs *Pyramidula tetragona*
- C. Seta greatly exserted beyond perichaetial leaves; calyptra sheathing but not plicate or prominently ribbed *Funaria microstoma*
- D. Setae straight without a tendency for adjacent ones to twist and tangle with one another; proximal portion of stem almost denuded of leaves or with leaves inconspicuous scales; capsules only very lightly sulcate with the depth of the sulcae less than the width between sulcae. *Funaria calvescens*
- D. Setae twisted and tangled with adjacent setae; proximal portion of stem with leaves gradually enlarged from base to the somewhat defined apical coma; capsules more deeply sulcate. *Funaria hygrometrica*

Grimmia Hedwig, 1801.

Mosses included in this section are mostly blackish to blackened green acrocarps with hyaline awns and lanceolate leaves. Unlike the awned members of the Pottiaceae, Encalyptaceae, and Hedwigiaceae, *Grimmia* is seldom papillose and those papillose members of the genus are papillose primarily by ornamentations on the lateral and end-walls of the laminal cells.

Species included in this key: all Grimmiaceae, except *Brachydontium* (Seligeriaceae)

- Brachydontium olympicum* (E. Britton) McIntosh & Spence*
- Coscinodon cribrosus* (Hedwig) Spruce*
- Coscinodon calyptratus* (Drummond) C. E. O. Jensen in Kindberg
- Grimmia alpestris* (Weber & D. Mohr) Schleicher
- Grimmia americana* E. B. Bartram*
- Grimmia anodon* Bruch & W. P. Schimper
- Grimmia anomala* Hampe in W. P. Schimper
- Grimmia arcuatifolia* Kindberg
- Grimmia caespiticia* (Bridel) Juratzka
- Grimmia donniana* Smith*
- Grimmia elatior* Bruch ex Balsamo & De Notaris*
- Grimmia hamulosa* Lesquereux
- Grimmia hartmanii* W. P. Schimper*
- Grimmia incurva* Schwägrichen*
- Grimmia laevigata* (Bridel) Bridel
- Grimmia leibergii* Paris
- Grimmia lesherae* H. C. Greven
- Grimmia lisae* De Notaris
- Grimmia longirostris* W. J. Hooker
- Grimmia mariniana* Sayre
- Grimmia mollis* Bruch & W. P. Schimper
- Grimmia montana* Bruch & W. P. Schimper

- Grimmia moxleyi* R. S. Williams in Holzinger
- Grimmia nevadensis* H. C. Greven
- Grimmia orbicularis* Bruch in Wilson
- Grimmia ovalis* (Hedwig) Lindberg
- Grimmia pilifera* Palisot de Beauvois*
- Grimmia plagiopodia* Hedwig
- Grimmia poecilostoma* Cardot & Sebillé
- Grimmia pulvinata* (Hedwig) J. E. Smith
- Grimmia ramondii* (Lamarck & A. P. de Candolle) Margadant
- Grimmia reflexidens* C. Müller Hal.
- Grimmia serrana* Muñoz, Shevock & Toren
- Grimmia shastae* H. C. Greven
- Grimmia tergestina* Tommasini ex Bruch & W. P. Schimper
- Grimmia torquata* Drummond
- Grimmia trichophylla* Greville
- Grimmia ungeri* Juratzka in Unger & Kotschy
- Grimmia unicolor* W. J. Hooker in Greville*
- Jaffueliobryum raui* (Austin) Thériot
- Jaffueliobryum wrightii* Sullivant in Sullivant & Lesquereux
- Schistidium strictum* (Turner) Loeske*
- Schistidium tenerum* (J. E. Zetterstedt) E. Nyholm

Work with *Grimmia* requires cross-sections made near the middle of a leaf. These cross-sections must be thin enough to turn over on their sides so that the anatomy of that section can be seen. Past work with *Grimmia* has emphasized the presence or absence of hyaline awns but those features are not completely reliable—almost any normally awned species can be found without awns. A plant can be said to have an hyaline awn even when only a few terminal cells on the leaf are hyaline. In California, *Grimmia* is perhaps our most widespread petricolous genus throughout all ecological regions in the state. *Grimmia*, a genus of 75–90 species world-wide is especially well-represented in California with several recently described species. Often a single rock outcrop will host multiple species of *Grimmia* even under what appears to be identical ecological conditions.

The three major genera of the Grimmiaceae are interestingly different in their ecological ranges. *Grimmia* is most common in the drier regions; *Racomitrium* is more common in the more coastal humid regions; and *Schistidium* is especially common in areas of intermittent flowing water and sheet drainages, mostly ones dry by early summer.

Among these three genera, recognition of *Racomitrium* is usually rather easy because of the strongly sinuose lateral walls of the laminal cells but some specimens of *Grimmia leibergii* and *G. trichophylla* may have sufficient sinuosity to allow for some confusion. The systylos and immersed capsules of *Schistidium* allow easy recognition of fertile plants but without sporophytes, however, distinction of *Grimmia* from *Schistidium* may be very difficult. The habitat of *Schistidium* mentioned in the previous paragraph allows field distinction of most species but *Grimmia mollis* and *G. hamulosa* may occupy the types of sheet drainages in high mountains that are the province of many species of *Schistidium*. In the field, most species of *Schistidium* can be recognized by a reddish wash unduplicated by any species of *Grimmia*. Another feature allowing field determination is the tendency of *Schistidium* to grow as loose cushions whose branch innovation are obvious without dissection. Most *Grimmia* produce cushions so dense as to obscure any branching. In the key which follows we have included some of the awned *Schistidium* but we have found that the muticous species of that genus can be keyed in the generic key that precedes these species keys.

- A. Dry plant with leaves very strongly crispate; margins serrate to dentate; sporophytes exserted, usually several per perichaetium. see *Ptychomitrium*
- A. Leaves not crispate, or, if so, with the margins entire; plant monosetous. B
- B. Leaves deeply concave, mostly with cucullate apices; consistently muticous. C
- B. Leaves without cucullate apices. D
- C. Leaves broadly ovate-oblong, with unistratose laminae; cells of lamina more than 10 μm broad. *Grimmia mollis*
- C. Leaves very narrowly oblong-lanceolate with multistratose laminae; cells less than 10 μm broad. *Grimmia unicolor**
- D. Leaves plicate above the base with the leaf cross-section showing a thickening along the length of the plica. E

- D. Leaves not plicate or with the plicae inconspicuous at extreme base, often on only one side of leaf. F
- E. Laminal cells bulging to papillose; capsule exserted; calyptra cucullate and smooth. *Grimmia caespiticia*
- E. Laminal cells with surface flat to weakly convex in cross-section; capsule immersed; calyptra mitrate to campanulate, plicate. *Coscinodon cribrusosus**
- F. Leaves spirally 3-ranked; leaf apices when dry spirally inflexed. *Grimmia torquata*
- F. Leaves not strongly ranked; leaf apices when dry outwardly directed or irregularly arranged. G
- G. Costa abruptly expanded and flattened in the unistratose basal portion of leaf; costa at base about ten cells wide in abaxial view; costa not at all grooved adaxially in distal portion of leaf; basal cells except for a few juxtacostal ones not at all elongate; alar cells numerous, mostly transversely elongate. *Grimmia laevigata*
- G. Costa not expanded and flattened, variously restricted to an adaxial channel but never so flattened; basal and alar cells not transversely elongate. H
- H. Cells of basal leaf margins with transverse walls not significantly thicker than lateral walls. I
- H. Cells of basal leaf margins with transverse walls markedly thicker than lateral, including marginal, walls. N
- I. Leaf margins recurved, at least near base on one side. J
- I. Leaf margins plane to erect. K
- J. Leaves somewhat crispate when dry; lamina unistratose with bistratose streaks and margins; median laminal cells smooth. *Grimmia incurva**
- J. Leaves not crispate; lamina bistratose throughout; median laminal cells bulging mammillose to papillose. *Grimmia elatior**
- K. Leaves falcate and somewhat homomallous; lamina bistratose to below leaf middle; leaves muticous. *Grimmia hamulosa*
- K. Leaves straight or nearly so; lamina unistratose or with streaks of bistratosities near apex; leaves usually with a prominent hyaline awn. L
- L. Leaves mostly less than 1.5 mm long, distally subulate with the costa filling essentially all of the subula; capsule exserted on an arcuate seta; peristome absent. *Brachydontium olympicum**
- L. Leaves longer, not so strongly subulate; capsule various but peristome present. M
- M. Leaves with bistratose margin mostly only one cell wide; leaf cross-section showing hourglass-shaped vertical walls with the cells deeper than wide and with elliptical lumina; calyptra large and mitrate to campanulate, plicate. *Coscinodon calyptratus*
- M. Leaves mostly with bistratose margin broader; leaf cross-section with vertical walls not hourglass-shaped and with the cells as deep as wide with angular lumina; calyptra cucullate and smooth. *Grimmia donniana**
- N. Leaves in cross-section with lamina immediately lateral to the costa only one cell layer thick but with the margin 3–6 cells thick; awn poorly developed or absent on most leaves. *Grimmia serrana*
- N. Leaves and awns not in all respects as above. O
- O. Leaves, including the perichaetial leaves, without hyaline awns; costa thick and angular or furrowed in cross-section. P
- O. Leaves with hyaline awns on at least the perichaetial leaves; costa thin, often not bulging on abaxial surface. R
- P. Costa grooved abaxially and appearing therefore to have a pair of abaxial lamellae; gemmae never present on leaf apices; plant dark greenish-brown. *Grimmia ramondii*
- P. Costa angular to rounded abaxially; gemmae usually present on leaf apices; plant deep green compared with most other members of the genus. Q
- Q. Leaves with longitudinal cuticular ridges, thus appearing papillose; gemmae yellow to green; costa rounded abaxially. *Grimmia anomala*
- Q. Leaves without such ridges; gemmae red-brown; costae angular on abaxial surface in cross-section. *Grimmia hartmanii**
- R. Costae in cross-section hardly thicker than lamina with the lateral margins poorly demarcated from the leaf lamina. S
- R. Costae in cross-section at least twice as thick as lamina with the lateral margins well demarcated. X
- S. Juxtacostal cells of leaf base more than 4:1, irregularly thickened to sinuose on the lateral walls; capsules exserted. *Grimmia ovalis*
- S. Juxtacostal cells of leaf base less than 4:1, with lateral walls evenly thickened; capsules immersed. T
- T. Leaf lamina unistratose throughout; hyaline awn on at least some of the leaves extending farther

- down the costa than down the margins; calyptra campanulate; perichaetial leaves larger than the adjacent vegetative leaves, never reduced to flaccid hyaline structures. U
- T. Leaf lamina bistratose throughout; hyaline awn arising from truncate apex of green leaf or somewhat decurrent; calyptra cucullate; perichaetial leaves reduced to flaccid and hyaline structures. V
- U. Leaves deeply concave without a semblance of a keel; hyaline awns mostly more than 1.5 times as long as the green portion of the leaf. *Jaffueliobryum rauli*
- U. Leaves somewhat keeled distally; hyaline awn similar in length to the rest of the leaf. *Jaffueliobryum wrightii*
- V. Capsule symmetric with the short seta straight and attached centrally to the capsule base. *Grimmia tergestina*
- V. Capsule asymmetric with the short seta curved and attached to one side of the capsule base. W
- W. Plant autoicous with the perigonia obvious in leaf axils immediately below the terminal perichaetia. *Grimmia americana**
- W. Plant dioicous with perigonial plants usually in separate cushions from the perichaetial plants. *Grimmia poecilostoma*
- X. Leaf margins plane to erect throughout with not even a trace of basal recurvature. Y
- X. Leaf margins recurved on at least one side at least near base. AH
- Y. Leaves linear to narrowly linear-lanceolate, mostly with parallel sides; capsule eperistomate, immersed to barely emergent; perichaetial leaves markedly larger and broader than adjacent vegetative leaves. Z
- Y. Leaves lanceolate with costa not filling apex; capsule exserted; perichaetial leaves mostly not well differentiated; peristome present or absent. AA
- Z. Distal portion of leaf with costa filling more than ½ of leaf width; leaf not deeply grooved on adaxial side of costa in the distal portion of leaf. *Grimmia mariniana*
- Z. Distal portion of leaf with costa more narrow; leaf deeply grooved on adaxial side of costa in the distal portion of the leaf. *Grimmia nevadensis*
- AA. Leaves deeply keeled at the base with the broad costa occupying about ¼ of that base; cells finely papillose; internal basal cells rectangular with sinuose lateral walls. *Grimmia lesherae*
- AA. Leaves, if keeled, with that keeling primarily in their distal ½; costa not so broad; leaf cells mostly smooth; internal basal cells various. AB
- AB. Leaves deeply concave with the area near the costa seen in cross-section rising almost vertically from insertion on the costa and forming a deep channel. *Grimmia reflexidens*
- AB. Leaves without such a channeled central area along the costa. AC
- AC. Leaf unistratose throughout or with a single row of bistratosity at margin; capsules immersed. AD
- AC. Leaf limb distal to the region of rectangular basal cells mostly several layers thick; capsules emergent to exserted. AE
- AD. Peristome present; leaves concave with cross-section at mid-leaf almost flat. *Grimmia plagiopodia*
- AD. Peristome absent; leaves strongly keeled with cross-section at mid-leaf V-shaped. *Grimmia anodon*
- AE. Median laminal cells bulging on both surfaces as seen in cross-section. *Grimmia alpestris*
- AE. Median laminal cells flat on both surfaces. AF
- AF. Costa cross-section showing well-defined abaxial and adaxial epidermises and showing an abaxial stereid band; distal portion of leaf with multicellular, globose gemmae on adaxial surface. *Grimmia shastae*
- AF. Costa cross-section without such epidermises or stereid bands; epiphyllous gemmae not present. AG
- AG. Operculum short obliquely-rostrate; capsule exserted; juxtacostal cells of leaf base rectangular, more than 3:1; plants dioicous. *Grimmia montana*
- AG. Operculum apiculate and not oblique; capsule emergent but barely so; juxtacostal cells of leaf base very short rectangular; plants autoicous. *Grimmia ungeri*
- AH. Costa in cross-section three or more cells wide between the insertion of the laminae on the adaxial surface. AI
- AH. Costa in cross-section only 2 cells wide on adaxial surface. AM
- AI. Laminal cells and abaxial cells of costa high papillose; plant with a strongly reddish cast; sporophytes immersed, systylious. *Schistidium strictum**
- AI. Leaf lamina and costa not papillose; plant deep green to black; sporophytes exserted on a straight to arcuate seta, not systylious. AJ

- AJ. Juxtacostal cells of leaf base with even thickening of their lateral walls. *Grimmia lisae*
AJ. Juxtacostal cells of leaf base somewhat sinuose or with nodular thickenings on their lateral walls. AK
AK. Costa near its apex with lamina on each side only 1–5 cells wide with the leaf therefore appearing subulate; leaves in distal one-half sharply keeled with cross-section appearing V-shaped. *Grimmia arcuatifolia*
AK. Leaves lanceolate, not at all subulate; leaves bluntly keeled and U-shaped in cross-section in distal one-half. AL
AL. Hyaline hair-point terete; seta straight; leaf margins not recurved in distal one-half, usually recurved only on one side. *Grimmia longirostris*
AL. Hyaline hair-point flat; seta curved; leaf margins recurved to revolute on both sides, usually above leaf middle. *Grimmia leibergii*
AM. Leaves bistratose in much of upper leaf, often with bistratosities filling the distal regions. . . AN
AM. Leaves unistratose except at margin; awn smooth or nearly so. AP
AN. Leaves deeply concave with the area near the costa seen in cross-section rising almost vertically from insertion on the costa and forming a deep channel; capsules exerted. *Grimmia reflexidens*
AN. Leaves without such a channeled central area along the costa; capsules immersed. AO
AO. Leafy stems less than 0.5 mm wide and mostly less than 25 mm long; leaves less than 1 mm long; plants forming wiry chestnut-brown turfs on seepages at high elevations; capsules systylious. *Schistidium tenerum*
AO. Plants and leaves larger; plant green to blackish-green primarily growing on median elevation rocks, not in seepages; capsules not systylious. *Grimmia pilifera**
AP. Leaves lanceolate, broadest near the base. AQ
AP. Leaves elliptic to oblong, broadest near the middle, not at all crispate when dry. AR
AQ. Leaves somewhat crispate when dry; plant green to blackish-green; median supra-alar cells with sinuose walls; capsules inserted on a cygneous seta, not systylious. . . *Grimmia trichophylla*
AQ. Leaves not crispate; plant with a reddish blush, especially near leaf bases; median supra-alar cells not sinuose on lateral walls; capsules immersed and systylious. see *Schistidium*
AR. Perigonia located in leaf axils a few leaves below the perichaetium; calyptra mitrate, covering little more than the operculum; peristome teeth mostly entire. *Grimmia pulvinata*
AR. Perigonia terminal on branch stems; calyptra cucullate; peristome teeth cribose, often irregularly split. AS
AS. Hyaline awn present only on perichaetial leaves with vegetative leaves bluntly rounded; basal juxtacostal cells with straight lateral walls. *Grimmia moxleyi*
AS. Hyaline awn present both on perichaetial and vegetative leaves; basal juxtacostal cells with nodulose walls. *Grimmia orbicularis*

***Gymnostomum* Nees & Hornschuch in Nees, Hornschuch, & Sturm, 1823.**

In this key we treat acrocarpous, costate and pluripapillose plants mostly with entire and plane margins. These plants are usually calciphiles or on desert seepages, especially along crevices of shaded rock underhangs. One of the most unusual features of these plants is the great variability of size and shape of the basically isodiametric cells.

Species included in this key: all are Pottiaceae except *Zygodon* (Orthotrichaceae)

- Anoectangium aestivum* (Hedwig) Mitten*
Eucladium verticillatum (Hedwig in Bridel) Bruch & W. P. Schimper
Gymnostomum aeruginosum J. E. Smith*
Gymnostomum calcareum Nees & Hornschuch
Hymenostylium recurvirostre (Hedwig) Dixon
Molendoa sendtneriana (Bruch & W. P. Schimper) Limpricht
Zygodon rupestris W. P. Schimper ex Lorentz

Gymnostomum is restricted to calcareous, usually limestone, habitats throughout the state. While it can form small tufts of only a few loosely placed plants, it almost always forms large and very tight, somewhat glaucous, cushions. In areas of long-duration seeps over limestone, it may form cushions several square meters in size. The larger cushions of *Gymnostomum* when vertically split often reveal internal layering that may represent annual increments of growth. This plant can be confidently identified when one sees the rather short leaves with plane margins and papillose leaf cells. *Anoectangium* has these same features but it is not yet found in the state. A field character for this latter genus is the hint of tristichous leaf arrangement, a feature not present in *Gymnostomum*. Another useful field character for *Gymnostomum* is

the tendency for colonies to dry and crack into rectangular blocks like dried clay. There is great diversity of opinion on whether to recognize the two Western North American species of *Gymnostomum*. After much hesitation, we suggest that all the Californian material that we have examined falls into *G. calcareum*, and we find the nearest localities for *G. aeruginosum* in Washington State. We have become convinced of their distinction not only by the cell size differences and by the larger plant typical of *G. aeruginosum* but, more importantly, by the looser clones of that latter species.

- A. Leaves terminating in a single elongate and more or less hyaline cell that differs strongly from the isodiametric subapical cells; cells of leaf lamina with multiple, sharp and discrete papillae; axils of younger leaves usually with stalked, elliptical, septate gemmae. *Zygodon rupestris*
- A. Leaf apices acute but mostly without a differentiated apical cell; cells of leaf lamina with multiple, blunt papillae that seem to merge with neighboring papillae in a complex of roughenings; gemmae scarce, not stalked. B
- B. Leaf margin at junction between the basal and upper laminal cells with several teeth. *Eucladium verticillatum*
- B. Leaf margin entire throughout. C
- C. Margin recurved at extreme basal margin on at least one side of some of the leaves; extreme distal cell of leaf pellucid and somewhat enlarged. *Hymenostylium recurvirostre*
- C. Margins plane throughout; distal cell of leaf not so differentiated. D
- D. Costa on adaxial surface with quadrate cells little different from adjacent laminal cells; leaves not adaxially grooved; leaves spirally arranged along stem. E
- D. Costa with elongate cells on adaxial surface; leaf deeply grooved by ascending lamina on each side of costa on at least the distal one-half; perichaetia lateral; leaves obscurely tristichous. . . . F
- E. Costa less than 50 μm wide at base; cells near leaf apex 7–8 μm wide. *Gymnostomum calcareum*
- E. Costa more than 60 μm wide at base; cells near leaf apex more than 10 μm wide. *Gymnostomum aeruginosum**
- F. Leaves concave, especially near apex; costa of well developed leaves with two stereid bands. *Molendoa sendtneriana*
- F. Leaves keeled along costa; costa with only one stereid band. *Anoetangium aestivum**

Hamatocaulis* Hedenäs, 1989. see *Drepanocladus

Hamatocaulis vernicosus (Mitten) Hedenäs

Hamatocaulis is a generic segregate from the larger genus of aquatic to semi-aquatic pleurocarps, *Drepanocladus*. Its leaves are considered plicate but that feature may be difficult to demonstrate on many specimens. However, a careful removal of the leaves, including the bases, from a portion of a stem will reveal one or two small kinks in the leaf scar somewhere between the costa and the leaf margin on both sides of the leaf. The leaves, while falcate, are much broader at the base than most leaves that are considered falcate. That base, on the intact stem, peculiarly is oriented erect and close to the stem with only the distal half of the leaf giving the falcate and secund appearance. *Hamatocaulis* is restricted to bogs and fens.

***Hedwigia* Palisot de Beauvois, 1804.**

The mosses treated in this section are julaceous with ecostate leaves and high papillose median laminal cells. With the exception of *Braunia*, these plants have hyaline awns.

Species included in this key: all Hedwigiaceae

- Braunia secunda* (W. J. Hooker) Bruch & W. P. Schimper in Bruch & W. P. Schimper*
- Hedwigia ciliata* (Hedwig) Palisot de Beauvois*
- Hedwigia detonsa* (Howe) W. R. Buck & Norris
- Hedwigia stellata* Hedenäs
- Pseudobraunia californica* (Lesquereux) Brotherus

In California, we have two genera of the Hedwigiaceae, and these both are immediately recognized as petricolous mosses with hyaline awns and deeply concave, ecostate leaves on a julaceous stem. Those few characters allow immediate and unambiguous recognition.

- A. Leaves without hyaline awns; base of leaf with small plications. *Braunia secunda**
- A. Leaves with hyaline awns, wrinkled but not plicate when dry. B
- B. Median leaf cells with unbranched papillae that appear circular to short-elliptic from surface

- view; awn long and flexuose, often caducous in older leaves, uniseriate for most of its length; capsule exerted. *Pseudobraunia californica*
- B. Median cells with branched papillae that appear stellate in surface view; awn decurrent and not flexuose or caducous, several cells broad to near the apex; capsules immersed. C
- C. Abaxial surface of some of the upper laminal cells with more than 2 papillae; apical cell of awn usually truncate and coronate papillose. *Hedwigia ciliata**
- C. Abaxial surface of upper laminal cells consistently with only 1–2 papillae; apical cell of awn pointed with papillae seriate. D
- D. Perichaetial leaves without marginal cilia; awns of vegetative leaves with spinose teeth both on the margins and on the dorsal surfaces; the perichaetial leaves abruptly larger than the vegetative leaves of adjacent branches. *Hedwigia detonsa*
- D. Perichaetial leaves with ciliate margins; dry plant with awns of vegetative leaves erect or nearly so; awns of vegetative leaves serrulate or even entire, never spinose on dorsal surfaces; the large perichaetial leaves only gradually differentiated from the smaller vegetative leaves. *Hedwigia stellata*

Helodium* Warnstorf, 1905. see *Hylocomium

Helodium blandowii (Weber & D. Mohr) Warnstorf

Helodium has only recently been found in California in several sites primarily on the east side of the Sierra. In the field, it is an immediately recognizable plant in its bog and fen habitats. We have found that the pale coloration sometimes suggests *Sphagnum* to the uninitiated. No confusion is possible, however, once one sees its closely pinnate growth habit (note the fasciculate branching of *Sphagnum*). One of the most peculiar microscopic features of *Helodium* is the placement of much lobed and filamentous-tipped paraphyllia. While some paraphyllia are inserted on the stem, others are inserted on the margins of the leaf bases.

Hennediella* Paris, 1896. see *Tortula

Hennediella heimii (Hedwig) Zander

Hennediella stanfordensis (W. C. Steere) Blockeel

Our species of *Hennediella* have C-shaped papillae on short rectangular cells with rounded lumina. This combination suggests a member of the Pottiaceae rather near to *Syntrichia* or *Tortula*. One might look in *Microbryum* but *Hennediella* has leaves that are too spreading for that bulbiform genus. The diagnostic feature for the genus in California is the trace of a limbidium. That limbidium is very obvious in *H. stanfordensis* but it consists of only a few somewhat elongate cells in *H. heimii*. Both species are seriate papillose on the limbidial cells—a feature very infrequently encountered among California acrocarpous mosses.

Herzogiella* Brotherus, 1925. see *Hypnum

Herzogiella seligeri (Bridel) Iwatsuki

Herzogiella striatella (Bridel) Iwatsuki

Herzogiella in California comprises two species generally included in older works under *Plagiothecium*. These two species are restricted to montane sites in northwestern California. They are recognizably complanate but that complanation may be obscured by a strong tendency toward a secund or homomallous condition. This pattern allows easy recognition of this pleurocarpous and ecostate moss. A quick examination of the upper leaf margin for the rather strong serration of the acuminate apex will further confirm a field identification. Under a compound microscope, the pattern of strongly porose basal cells of *Herzogiella* is unique among the plants previously placed in the broadly defined genus, *Plagiothecium*. The capsules are unusual among the Hypnaceae in being sulcate.

***Heterocladium* Bruch & W. P. Schimper, 1852.**

Mosses treated here have short double costae, variously papillose cells, and regularly pinnate branching. Species included in this key: all Pterigynandraceae

Heterocladium dimorphum (Bridel) W. P. Schimper in Bruch & W. P. Schimper

Heterocladium macounii Best

Heterocladium procurrens (Mitten) A. Jaeger*

Myurella julacea (Schwägrichen in Schultes) Bruch & W. P. Schimper
Pseudoleskeella tectorum (Funck ex Bridel) Kindberg ex Brotherus

Work on *Heterocladium* requires careful attention to the stem and branch heterophylly. Carefully note in the key that follows whether stem or branch leaves are being described. *Heterocladium* is a plant of moist rock outcrops in the northwest of the state. Only *H. macounii* is likely; *H. dimorphum* is known only as an introduction in San Francisco; *H. procurrens* is abundant in Oregon not far from the California border.

- A. Cells of branch leaves pluripapillose; plant usually more or less pinnately branched; stems papillose. *Heterocladium macounii*
- A. Cells of branch leaves unipapillose to smooth; stems irregularly branched, not papillose. B
- B. Branch leaves obtuse to minutely apiculate. *Myurella julacea*
- B. Branch leaves acute to acuminate. C
- C. Plants irregularly branched. *Pseudoleskeella tectorum*
- C. Plants pinnately branched. D
- D. Cells of stem leaves smooth. *Heterocladium procurrens**
- D. Cells of stem leaves unipapillose. *Heterocladium dimorphum*

Homalia* Bridel, 1827. see *Neckera

Homalia trichomanoides (Hedwig) W. P. Schimper in Bruch & W. P. Schimper*

Homalia is not yet found in California. In Washington State it is not uncommon on trees and calcareous rocks from sea level to montane elevations. It can readily be placed in the Neckeraaceae on the basis of the blunt and costate, complanate leaves with short cells. One might think of *Porotrichum* on first encountering *Homalia*, but the dentate margin of the former plant differs radically from the finely serrulate margin of *Homalia*.

***Homalothecium* W. P. Schimper in Bruch & W. P. Schimper, 1851.**

Mosses treated in this section are costate pleurocarps of mesic habitats. They have strong costae that extend into the base of the acumen. The leaves are plicate with several plicae on each side of the costa.

Species included in this key: all Brachytheciaceae, except *Tomentypnum* (Campyliaceae)

- Homalothecium aeneum* (Mitten) E. Lawton
- Homalothecium arenarium* (Lesquereux) E. Lawton
- Homalothecium fulgenscens* (Mitten ex C. Müller Hal.) E. Lawton
- Homalothecium nevadense* (Lesquereux) Renauld & Cardot
- Homalothecium nuttallii* (Wilson) A. Jaeger
- Homalothecium pinnatifidum* (Sullivant & Lesquereux) E. Lawton
- Tomentypnum nitens* (Hedwig) Loeske*
- Trachybryum megaptilum* (Sullivant) W. B. Schofield

The genus *Homalothecium* is here viewed as including *Camptothecium* Bruch & W. P. Schimper. Dixon and Jameson (1924) pointed out the variation in capsule form in the usually symmetric-capsuled *Homalothecium* as opposed to the usually arcuate-capsuled *Camptothecium*. We concur in that observation. The members of both *Homalothecium sensu stricto* and *Camptothecium sensu stricto* share an overall field appearance: large mats of golden-green plants with strongly plicate, costate leaves. The dry plants of *Homalothecium sensu lato* consistently have the leaves somewhat twisted around the stem so as to give the leafy stem a corded appearance like that of a cotton rope. While we have lumped *Homalothecium* and *Camptothecium* into a single genus, we have followed other workers in recognizing two separate genera on the basis of rectangular, thick-walled and pitted alar cells: *Tomentypnum* and *Trachybryum*. The six California species in our definition of *Homalothecium* are easily recognized in the field. *H. arenarium* is the one representative of the genus without the characteristic golden-green coloration. North of the San Francisco Bay area, *H. arenarium* is primarily found on sand-dunes but, to the south, it moves out onto the soil of open forests and scrub. The remaining species of California *Homalothecium* occur on tree trunks and rock outcrops.

- A. Alar cells rectangular and thick-walled; stems plumose and loosely ascending; leaves 3–5 mm long. B
- A. Alar cells at least in part quadrate; main stem prostrate; leaves smaller. C
- B. Plants of high-elevation calcareous bogs; older portions of stems densely cloaked with clusters

- of brown rhizoids that are inserted on the abaxial surface of the leaf near the costa. *Tomentypnum nitens**
- B. Plants of soil in mesic forests; rhizoids not so densely arranged, inserted on stem. *Trachybryum megaptitulum*
- C. Quadrate alar cells reaching costa; costa with a number of spines closely arranged on the distal portion; costa extending to near the base of the acumen; dry branches not markedly hamate. ... *Homalothecium arenarium*
- C. Alar cells not reaching costa; spines on costa inconspicuous, mostly single; length of costa usually shorter; dry branches markedly hamate. D
- D. Differentiated alar cells quadrate to short-rectangular, up to 15 on margin and 10 along the base; quadrate alar cells extending farther along margin than along immediate inframarginal regions. ... E
- D. Differentiated alar cells fewer; immediate margin of alar region with elongate cells. F
- E. Leaves long-decurrent; main stems up to 15 cm long. *Homalothecium* species A
- E. Leaves not or very little decurrent, plant smaller. *Homalothecium pinnatifidum*
- F. Larger stem leaves often with a somewhat auriculate base; alar cells mostly elongate but with a few quadrate cells; urn 2.4–2.8 mm long with a short-rostrate operculum over 1 mm long; mostly on trees near the coast. *Homalothecium fulgescens*
- F. None of the stem or branch leaves at all auriculate; alar cells mostly quadrate; urn shorter with operculum conic and shorter; ecology various. G
- G. Leaves with several marginal teeth near junction of alar region with more distal region; plant usually very regularly pinnate, often with flagelliform caducous branchlets; stem leaves mostly less than 2 mm long; plant epiphytic on trees near the coast. *Homalothecium nuttallii*
- G. Leaves without such peribasal teeth; plant pinnate but often obscurely so, without caducous branchlets; stem leaves larger; range and geography various.
- H. Alar cells rather obscure under low magnifications of the compound microscope with alar region more opaque than surrounding cell regions. *Homalothecium nevadense*
- H. Alar cells with outlines clear under low magnification; alar region not so opaque. *Homalothecium aeneum*

Homomallium* (W. P. Schimper) Loeske, 1907. see *Hypnum

Homomallium mexicanum Cardot

Homomallium mexicanum, a species of Mexico and adjacent portions of Texas to Arizona, was recently found in southeastern California. It is an ecostate pleurocarp with a long acumen and with numerous quadrate alar cells. Unlike *Hypnum*, it is not falcate although the leaves are somewhat homomallous.

***Hookeria* Smith, 1808.**

The mosses keyed in this section combine complanate and ecostate leaves with median cell size such that one can see those cells with the naked eye.

Species included in this key: all Hookeriaceae

- Hookeria acutifolia* W. J. Hooker & Greville*
- Hookeria lucens* (Hedwig) J. E. Smith

Hookeria is our single generic representative of a large tropical complex. *Hookeria lucens* is restricted to the perhumid areas of coastal and mountainous northern California. It is especially common on organic soil of trail banks and in small organic soil depressions of shallow winter water accumulation. One of the more interesting features of both the species of western North America is the production of rhizoids from the tips of the leaves. Even when rhizoids are absent, one can find in the leaf apices groups of radically shorter and thinner walled cells that function as “nematogons,” cells of the leaves that are capable of producing rhizoids. *Hookeria acutifolia* is occasionally found in Washington State on mineral soil of vertical creek banks. It should be looked for on similar banks in northern California.

- A. Leaf apex obtuse. *Hookeria lucens*
- A. Leaf apex acute. *Hookeria acutifolia**

Hygroamblystegium* Loeske, 1903, *nomen conservandum*. see *Amblystegium

Hygroamblystegium tenax (Hedwig) Jennings

Our one species of *Hygroamblystegium* can almost be recognized by touch. *Hygroamblystegium tenax*

is a small leaved aquatic and pleurocarpous moss whose very broad costa and stiffly arching stems give it an overall very coarse feel. No other moss combines a regularly branching pattern with spreading narrowly lanceolate leaves whose costa fills perhaps $\frac{1}{4}$ – $\frac{1}{5}$ of the leaf base. The very short cells have elliptical lumina mostly about 3:1 and the cell walls are usually rather thick. *Hygroamblystegium tenax* can be looked for in thin seepages over outcrops throughout much of the hotter and drier portions of the state. It is especially common on overflowing portions of concrete water-troughs.

***Hygrohypnum* Lindberg, 1872.**

Mosses included in this section are aquatic pleurocarps mostly growing tightly adhering to rocks in flowing water. They have costae of various lengths that usually end below mid-leaf. The immediate leaf apex is blunt although many species seem acute to even acuminate when viewed in more gross detail.

Species included in this key: all Campyliaceae

- Hygrohypnum alpinum* (Lindberg) Loeske
- Hygrohypnum bestii* (Renauld & Bryhn) Brotherus
- Hygrohypnum cochlearifolium* (Venturi in De Notaris) Brotherus
- Hygrohypnum duriusculum* (De Notaris) Jamieson
- Hygrohypnum luridum* (Hedwig) Jennings
- Hygrohypnum molle* (Hedwig) Loeske
- Hygrohypnum ochraceum* (Turner ex Wilson) Loeske
- Hygrohypnum smithii* (Swartz in Liljeblad) Brotherus
- Hygrohypnum styriacum* (Limpricht) Brotherus

Hygrohypnum is a genus almost restricted to rocks in rapidly flowing streams. The majority of our species will be found in alpine to upper montane elevation forests but occurrences in lower elevation, unpolluted streams are possible. When one examines this aquatic, petricolous and pleurocarpous moss, one should look for a distally or even basally forked costa, and one should note blunt leaves whose apices have shortened cells in an apex that can overall be bluntly rounded or even acuminate. It should be noted here that a number of leaves often must be examined for the forking of the costa. It should further be noted that *Hygrohypnum smithii* will only occasionally show costal forking, and often the single costa will extend to $\frac{3}{4}$. This species of the genus is, however, easily determined in the field by its orbicular and spreading leaves. *Platyhypnidium riparioides* is somewhat similar in habitat, leaf shape and costal length but this latter moss has strongly serrate to denticulate leaf margins from base to apex compared with the mostly entire margins of *H. smithii*.

The key below opens with *Hygrohypnum ochraceum*, a plant that can have straight or strongly falcate-secund leaves; a plant that can be complanate or almost julaceous. Its diagnosis under the compound microscope is, however, easy: the presence of a hyaloderm can be determined by a stem cross-section, or one can even rely simply on the fact that portions of the hyaloderm can usually be seen on leaves scraped from the stem for viewing.

One of the serious problems with collection of *Hygrohypnum* relates to the close adherence of the plant to rocks under rapidly flowing water. This often results in small and badly fragmented collections. We find removal of the plant with a putty-knife to be fairly successful.

- A. Stems and branches with a hyalodermis. *Hygrohypnum ochraceum*
- A. Outer cortex of stems and branches thick-walled. B
- B. Leaves falcate or some leaves on the same or different stems within the same specimen falcate. C
- B. Leaves all straight, sometimes secund. D
- C. Alar cells undifferentiated from adjacent cells; leaf apex abruptly acuminate.
- *Hygrohypnum styriacum*
- C. Alar cells small, quadrate to short-rectangular, incrassate; leaf apex acute. . . *Hygrohypnum luridum*
- D. Leaves with a single marginal, sometimes incomplete, row of marginal cells broader and thinner walled than more interior cells; these marginal leaf cells 60 μ m long or longer; leaves mostly more than 1.5 mm long. *Hygrohypnum bestii*
- D. Marginal leaf cells not so differentiated; leaves mostly smaller. E
- E. Costa on most leaves single, stout, extending to mid-leaf or slightly beyond, forked or short and double on smaller leaves; alar cells quadrate and incrassate; vegetative leaves less than 1 mm long. F
- E. Costa short and double, or longer and distally forked; alar cells variation; leaves mostly longer. G
- F. Leaves broadly ovate, about 1.5:1, somewhat concave. *Hygrohypnum smithii*

- F. Leaves orbicular, so concave as to describe a hemisphere. *Hygrohypnum cochlearifolium*
- G. Leaves orbicular, to 1.2:1. H
- G. Leaves mostly about 1.5:1. J
- H. Alar cells undifferentiated or with the few quadrate or short-rectangular cells incrassate or thin-walled. *Hygrohypnum molle*
- H. Alar cells clearly differentiated, either thin-walled or incrassate. I
- I. Alar cells thin-walled, usually hyaline, enlarged, rounded rectangular, forming a rectangular group whose long axis parallels the leaf margins; median leaf cells not at all prorate; inner perichaetial leaves prorate on the abaxial surface near the apex; dry plant soft to the touch. *Hygrohypnum alpinum*
- I. Alar cells incrassate, clearly pigmented in older leaves, quadrate, short rectangular or irregular, forming an irregular group, median leaf cells uniformly prorate on distal ends; inner perichaetial leaves smooth; dry plant harsh to the touch. *Hygrohypnum duriusculum*
- J. Alar cells clearly differentiated, smaller, incrassate and quadrate to short rectangular; leaf apex gradually contracted to an obtuse to bluntly rounded tip; plants autoicous. . . *Hygrohypnum luridum*
- J. Alar cells undifferentiated or not localized in a well-demarcated group; leaf apex abruptly acuminate, tapering to a slender tip; plants with dwarf males. *Hygrohypnum styriacum*

***Hylocomium* Bruch & W. P. Schimper in Bruch & W. P. Schimper, 1852.**

The plants included in this section are plumosely branched mosses mostly with the main axes decumbent to almost erect. Pinnately branched mosses with strictly prostrate main axes are treated under *Hypnum*. The mosses in this section are broadly called “feather mosses,” and nearly all the low elevation feather mosses of California are restricted to the extreme northern portions of the state. We note that such mosses either appear as large mats on the soil or litter or they are completely missing. We have speculated that a critical size is required for the clones of these mosses—a size that allows retention of sufficient moisture for survival through dry periods.

Species included in this key: all *Hylocomiaceae* except *Helodium* (*Helodiaceae*); *Kindbergia* and *Trachybryum* (*Brachytheciaceae*); *Ptilium* (*Hypnaceae*); *Rhytidium* (*Rhytidiaceae*) and *Thuidium* (*Thuidiaceae*)

- Helodium blandowii* (Weber & D. Mohr) Warnstorf
- Hylocomium splendens* (Hedwig) Bruch & W. P. Schimper
- Kindbergia oregana* (Sullivant) Ochyra
- Kindbergia praelonga* (Hedwig) Ochyra
- Pleurozium schreberi* (Bridel) Mitten*
- Ptilium crista-castrensis* (Hedwig) De Notaris*
- Rhytidiadelphus loreus* (Hedwig) Warnstorf
- Rhytidiadelphus squarrosus* (Hedwig) Warnstorf
- Rhytidiadelphus subpinnatus* (Lindberg) T. Koponen*
- Rhytidiadelphus triquetrus* (Hedwig) Warnstorf
- Rhytidiopsis robusta* (W. J. Hooker) Brotherus
- Rhytidium rugosum* (Hedwig) Kindberg*
- Thuidium recognitum* (Hedwig) Lindberg*
- Trachybryum megaptilum* (Sullivant) W. B. Schofield

Hylocomium splendens may produce more total biomass than any other moss in the world. It is found throughout arctic and cool temperate regions of Eurasia and North America, and it even shows discontinuities in some similar parts of the Southern Hemisphere. Despite all this abundance, and despite its great abundance even in nearby areas of Oregon and Washington, *Hylocomium splendens* has been found in only three sites in extreme northern parts of California. It is an immediately recognizable moss that produces repeatedly pinnately branched with strong heterophylly between the lanceolate leaves of the main upwardly arching stem and the concave and ovate to almost orbicular tiny leaves of all other orders of branching. It is commonly called the stair-step moss because of the pattern of new pinnate fronds of each year arising from central portions of the main stem of the previous year’s growth.

- A. Costa single and extending considerably above mid-leaf. B
- A. Costae double, ending at or below mid-leaf, sometimes almost absent. G
- B. Paraphyllia present, abundant on larger stems. C
- B. Paraphyllia absent. D
- C. Leaves plicate or wrinkled; paraphyllia attached to leaf bases and to stems, lobed with the lobes narrowly lanceolate to linear; plant of bogs or fens. *Helodium blandowii*

- C. Leaves not plicate; paraphyllia not attached to leaf bases but rather on stem, lobed into uniseriate filaments with the ultimate cell coronate-papillose; plants of mesic sites. . . . *Thuidium recognitum**
- D. Leaves strongly heterophyllous with stem leaves relatively broader and more decurrent, markedly larger than branch leaves; stem leaves strongly spreading to almost squarrose. E
- D. Leaves not so heterophyllous; stem leaves, if spreading, similar in orientation to branch leaves. . . F
- E. Plant regularly plumose with a single main stem from which arises shorter, nearly unbranched, lateral stems; plant mainly of coastal moderately low elevation sites. *Kindbergia oregana*
- E. Plant irregularly branched or tri- to tetra-pinnate; plant mainly of higher elevation, or of deeply shaded sites. *Kindbergia praelonga*
- F. Leaves strongly rugose. *Rhytidium rugosum**
- F. Leaves closely many times plicate. *Trachybryum megaptilum*
- G. Branched paraphyllia present and densely arranged on stems and branches. H
- G. Paraphyllia absent. I
- H. Plant regularly many times pinnately branched with the branches arranged in a single plane; leaves of ultimate branches broadly ovate, mostly less than 1 mm long. . . . *Hylocomium splendens*
- H. Plant sparingly and irregularly branched with the leaves of the branches not significantly smaller than those of the stems, mostly about 4 mm long. *Rhytidiopsis robusta*
- I. Leaves bluntly rounded at apex, never plicate or squarrose. *Pleurozium schreberi**
- I. Leaves acute to acuminate at apex, often plicate or squarrose. J
- J. Costa very short to inconspicuous, double and only a few cells long. . . . *Ptilium crista-castrensis*
- J. Costa double and at least one branch extending to mid leaf. K
- K. Leaves falcate-secund, ascending or weakly spreading, plicate, not at all papillose or prorate; tips of main stems arched downward toward the substratum. *Rhytidiadelphus loreus*
- K. Leaves not falcate, squarrose or broadly spreading, if plicate, the cells sharply prorate above mid-leaf; tips of main stems of well developed plants mostly ascending. L
- L. Leaves strongly plicate; cells sharply prorate at least above mid-leaf. . . . *Rhytidiadelphus triquetrus*
- L. Leaves not plicate; cells smooth. M
- M. Plant of lawns and other anthropogenic sites, pinnate but with the branches rather distantly spaced. *Rhytidiadelphus squarrosus*
- M. Plant of natural bogs, carrs, and other wet places; branching inserted regularly in the axils of every third or fourth leaf on each side of stem. *Rhytidiadelphus subpinnatus**

Hymenostylium* Bridel, 1827. see *Gymnostomum

Hymenostylium recurvirostre (Hedwig) Dixon

Hymenostylium in California is found on calcareous seepage along creeks and roads. It often is associated with tufa deposits. The erect and unbranched stems have lanceolate leaves with pluripapillose cells, and those leaves are strongly reflexed to almost squarrose when moist. The great variation in cell morphology within a single leaf reminds one of the *Weissia*, *Anoetangium* group within the Pottiaceae but the slightly recurved leaf margin is anomalous there. A cross-section of the stem will show thin-walled medullar cells throughout the center with no central strand.

***Hypnum* Hedwig. nomen conservandum**

The mosses keyed in this section are ecostate pleurocarps mostly with a prostrate growth habit. Most have falcate leaves or their leafy stems are hamate when dry. There is another group of ecostate pleurocarps with a prostrate growth habit but these are largely complanate. Such mosses are keyed under *Plagiothecium*.

Species included in this key: all Hypnaceae, except *Sematophyllum* (Sematophyllaceae)

- Breidleria pratensis* (Koch) Loeske*
- Calliergonella cuspidata* (Hedwig) Loeske
- Herzogiella seligeri* (Bridel) Iwatsuki
- Herzogiella striatella* (Bridel) Iwatsuki
- Homomallium mexicanum* Cardot
- Hypnum callichroum* Bridel*
- Hypnum circinale* W. J. Hooker
- Hypnum cupressiforme* Hedwig*
- Hypnum dieckii* Renauld & Cardot
- Hypnum fertile* Sendtner*
- Hypnum lindbergii* Mitten

Hypnum revolutum (Mitten) Lindberg

Hypnum subimponens Lesquereux

Hypnum vaucheri Lesquereux

Isopterygiopsis pulchella (Hedwig) Iwatsuki

Orthothecium chryseum (Schwägrichen in Schultes) W. P. Schimper in Bruch & W. P. Schimper*

Platydictya jungermannioides (Bridel) H. Crum

Ptilium crista-castrensis (Hedwig) De Notaris*

Sematophyllum adnatum (Michaux) E. Britton

Vesicularia vesicularis (Schwägrichen) Brotherus

The family Hypnaceae is easily recognized in the field by the combination of strongly falcate-secund leaves and very short costa. The presence or absence of an hyaloderm is especially important in this group. That feature is easily seen in a stem cross-section except that older stems have all the large and thin-walled cells of that hyaloderm collapsed. The resulting crenulate outer surface of the stem cross-section should be recognized as the product of such hyaloderm cell collapse. There is an unfortunate tendency for some of the hyaloderm cells to be removed with the leaves, and this may result in misinterpretations of those cells as alar or basal cells.

Inflated alar cells can be of special importance in *Hypnum*. As stated in the previous paragraph, problems arise when a plant has a hyaloderm. Uncertainty about where the extreme base of the leaf joins the hyalodermous stem, can be resolved with an examination of the bases of leaves not detached from the stem.

Another feature of importance in the *Hypnum* group is the difference between falcate leaves and circinate leaves. After removal of a leaf from the stem note the arc described by the mid-line of that leaf. Falcate leaves describe less than 180° of arc; circinate leaves describe more than 180° of arc.

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|--|-------------------------------------|
| A. Leaf margins recurved near the base or weakly reflexed nearly to apex, entire throughout or with a few weak teeth near the apex. | B |
| A. Leaf margins plane to ascending, clearly serrulate to serrate in distal ½. | E |
| B. Leaves with many parallel plications reaching above mid-leaf; median basal cells porose. | |
| | <i>Orthothecium chryseum</i> * |
| B. Leaves not plicate; median basal cells not or hardly porose. | C |
| C. Leaves only lightly concave with basal margins strongly recurved; alar cells quadrate in numerous rows, hardly inflated. | <i>Hypnum revolutum</i> |
| C. Leaves deeply concave with a weak reflexing along nearly the entire margin. | D |
| D. Alar cells quadrate but only gradually differentiated from median laminal cells; leaves with a very strong contraction to the acuminate apex. | <i>Homomallium mexicanum</i> |
| D. Alar cells strongly differentiated, inflated in one basal row of 2–4 cells; leaves rather gradually contracted to the acumen. | <i>Sematophyllum adnatum</i> |
| E. Leaves broadly ovate with median cells more than 12 µm broad, mostly less than 3:1; alar cells not differentiated. | <i>Vesicularia vesicularis</i> |
| E. Leaves lanceolate to ovate-lanceolate; median cells more narrow and relatively longer; alar cells various. | F |
| F. The majority of the alar cells quadrate and not inflated, sometimes with a few inflated cells at extreme angles; quadrate alar cells mostly extending more than 10 cells up margin. | G |
| F. Quadrate alar cells few, mostly subtended by several inflated cells at basal angles. | I |
| G. Leaves 0.5–1.0 mm long, not falcate but sometimes secund or homomallous, spreading and distant or concave and julaceous; alar cells quadrate in a well demarcated patch; multicellular gemmae often present in leaf axils. | <i>Platydictya jungermannioides</i> |
| G. Leaves larger, mostly falcate-secund; alar cells mostly few in a poorly demarcated patch; gemmae seldom present. | H |
| H. Leaves rather strongly concave, abruptly contracted to the acumen; median cells mostly less than 5:1; alar cells mostly more than 15 along margin. | <i>Hypnum vaucheri</i> |
| H. Leaves concave or not, gradually contracted to the acumen; median cells mostly more than 6:1; alar cells fewer than 12 along margin. | <i>Hypnum cupressiforme</i> * |
| I. Leaves strongly plicate and decurrent; plant so regularly pinnate and plumose as to have the branches parallel and contiguous; branches strongly hamate at apices. ... | <i>Ptilium crista-castrensis</i> * |
| I. Leaves lightly, or not at all, plicate; plant irregularly to regularly pinnate, never plumose and ascending; branches homomallous but not hamate. | J |
| J. Outer cortical cells of stem hyaline, thin-walled and enlarged relative to the adjacent inner cells. ... | K |
| J. Outer cortical cells not enlarged. | T |
| K. Alar cells strongly hyaline and inflated, mostly >5 times as broad as the adjacent laminal cells. | L |

- | | | |
|----|---|---|
| K. | Alar cells mostly not hyaline, less inflated, mostly with at least some wall thickening. | O |
| L. | Area of inflated and hyaline alar cells extending 3 or more cells up the margin and most of the way to mid-leaf; leaves homomallous but not very falcate. | M |
| L. | Area of inflated and hyaline alar cells inconspicuous and often left on stem with careless dissection, including only 1–2 rows of cells along the basal margin; plant mostly conspicuously falcate-secund. | N |
| M. | Apices of stems and major branches with the leaves so tightly imbricate as to form an acicular tip; stem leaves typically nearly entire even near apex; leaves straight, never falcate. | |
| | <i>Calliergonella cuspidata</i> | |
| M. | Stem and branch apices never acicular; stem leaves markedly serrulate near apex; leaves falcate-secund. | |
| | <i>Hypnum lindbergii</i> | |
| N. | Leaves rounded at the base in such a manner that the breadth of the insertion is only about ½ as great as the maximum leaf breadth immediately above that insertion; leaves straight to slightly falcate; leaf apices broadly acute to somewhat obtuse. | |
| | <i>Breidleria pratensis</i> * | |
| N. | Leaf bases not so rounded; breadth of insertion mostly more than ¾ as great as the maximum leaf breadth; leaves falcate to somewhat circinate; leaf apices so long and narrow as to be less than 8 cells broad within 3 cell lengths of apex. | O |
| O. | Leaves rather strongly serrulate; median basal cells strongly pitted; capsule sulcate. | P |
| O. | Leaves entire to serrulate; median basal cells not pitted; capsule smooth. | Q |
| P. | Leaves strongly decurrent with inflated rectangular cells in a triangular patch 3–5 cells wide distally. | |
| | <i>Herzogiella striatella</i> | |
| P. | Leaves not significantly decurrent (be careful that you do not interpret cells of the hyaloderm as decurrencies). | |
| | <i>Herzogiella seligeri</i> | |
| Q. | Stem leaves falcate from a somewhat erect base; basal marginal cells above the hyaloderm mostly quadrate to short rectangular, or with one or two somewhat inflated cells at extreme basal angles. | |
| | <i>Hypnum subimponens</i> | |
| Q. | Stem and branch leaves falcate to circinate from their bases; basal marginal cells above the hyaloderm cells of the stem enlarged relative to adjacent cells of the leaf. | R |
| R. | Leaves less than 2 mm long; plants growing on logs or tree bases. | |
| | <i>Hypnum fertile</i> | |
| R. | Leaves larger than 2 mm long; plants of soil or rock. | S |
| S. | Leaves serrulate at least at the apex; plants regularly pinnate with a red-brown wash on older stems and leaves; extreme leaf apex not filiform. | |
| | <i>Hypnum dieckii</i> | |
| S. | Leaves entire throughout; plants irregularly branched, green without a brownish wash; some leaves uniseriate for 2–3 cells at immediate apex. | |
| | <i>Hypnum callichroum</i> * | |
| T. | Quadrate alar cells numerous, mostly exceeding 15; plant olive-green and regularly pinnate, especially common on bark of coniferous trees. | |
| | <i>Hypnum circinale</i> | |
| T. | Quadrate alar cells fewer than 5; plant of soil and rocks mostly at high elevations. | |
| | <i>Isopterygiopsis pulchella</i> | |

Isopterygiopsis Iwatsuki, 1970. see *Hypnum*

Isopterygiopsis pulchella (Hedwig) Iwatsuki

Members of the genus *Isopterygiopsis* have complanate, ecostate leaves that are often somewhat falcate. It has been segregated from *Plagiothecium* because of the absence of either decurrent leaves or a hyaloderm.

Isopterygium Mitten, 1869. see *Plagiothecium*

Isopterygium tenerum (Swartz) Mitten

This is a species infrequently encountered in California but that scarcity may result primarily from its frequent pattern of depauperate growth among other mosses. It is our only complanate and ecostate moss with conspicuous clusters of filamentous pseudoparaphyllia, especially along main stems. It should be looked for in rock crevices in montane areas.

Isothecium Bridel, 1827.

Plants assigned to the genus *Isoetecium* are so variable in growth habit that even experienced bryologists have difficulty in field recognition features of the genus. In this genus, we have strongly julaceous examples, pendent and remotely leaved examples and plumosely branched examples. In contrast the genus *Isoetecium* is very easily recognized in microscopic examination: the alar region of densely chlorophyllous, mostly isodiametric cells is abruptly demarcated from the more elongate cells of the remainder of

the leaf. The character of leaf marginal toothing is unique among local mosses: above the leaf middle, the margin has a pattern of alternating large and small teeth such that every large tooth is flanked by two very small teeth.

Species included in this key: all Brachytheciaceae

- Isothecium cardotii* Kindberg
- Isothecium cristatum* (Hampe) H. Robinson
- Isothecium myosuroides* Bridel
- Isothecium obtusatum* Kindberg
- Isothecium spiculiferum* (Mitten) Renauld & Cardot
- Isothecium stoloniferum* Bridel

In the field, some of the species of *Isothecium* can be recognized by the olive-green coloration (often with a russet wash), the rather coarse serration near the leaf apex, and the rather strong differentiation of larger sheathing perichaetial leaves. Similar coloration, serration and perichaetial leaves are found in *Pterogonium gracile*. This latter species should not be mistaken in the field for any *Isothecium* because the regular branching pattern and hamate branch tips gives *Pterogonium* the appearance of a many-toed bird foot.

Species of *Isothecium* differ greatly from one another in degree of julaceous condition, in relative length/width ratio of the leaves, and in degree of plumose-dendroid branching. These differences between the species are, however, often blurred by many intermediate specimens. Allen (1983) did statistical studies on European materials that have mostly been called *Isothecium myosuroides*, and on North American materials under such names as *Isothecium stoloniferum*, *Isothecium cardotii*, *Isothecium spiculiferum*, and *Isothecium myurellum* Kindberg. While Allen made the decision not to recognize the latter four North American names, we have observed such a strong degree of ecological fidelity of the first three of those four species that we have decided to recognize them at the species level. In so doing, we have narrowed our concept of *I. myosuroides* among the California mosses.

- A. Leaves lingulate with an obtuse apex, mostly less than 1.5 mm long. *Isothecium obtusatum*
- A. Leaves ovate-lanceolate to very broadly ovate, not obtuse at apex, mostly larger. B
- B. Alar cells present in a triangular group that extends along margin nearly to mid-leaf; stems always strongly julaceous. *Isothecium cristatum*
- B. Alar cells present in a roundish, often concave group that seldom extends more than ten cells up the margin; stems sometimes not julaceous, often flagelliform. C
- C. Plants pendent to prostrate, hardly julaceous; alar region round in surface view, strongly excavate on larger leaves; most of the cells of distal region prorate. *Isothecium spiculiferum*
- C. Plants decumbent to ascending with branches strongly julaceous; alar region various; prorations on distal cells sparing or absent. D
- D. Acumen well-demarcated and occupying about 1/3 of leaf; distal portion of acumen with cells more elongate than in median region of leaf. *Isothecium myosuroides*
- D. Acumen only gradually defined; distal portion of leaves with cells similar to or shorter than median cells. E
- E. Plants plumose and erect to decumbent from an inconspicuous prostrate main axis; alar region round but not excavate; leaves concave, with acumen abruptly defined, mostly shorter than remainder of leaf. *Isothecium cardotii*
- E. Plants pinnately branched but only somewhat plumose; alar region strongly excavate; leaves concave, broadly ovate-lanceolate with acumen about as long as remainder of leaf. *Isothecium stoloniferum*

Iwatsukiella* W. R. Buck & H. Crum, 1978. see *Lescurea

Iwatsukiella leucotricha (Mitten) W. R. Buck & H. Crum*

Iwatsukiella has been found on coniferous tree trunks on a few fog-drenched ridges in Oregon. We view this tiny pleurocarpous moss as unlikely to occur in California. Among pleurocarpous mosses with hyaline awns, *Iwatsukiella* might possibly be confused with a very small *Claopodium* but the hyaline awned members of that genus occupy rock outcrops and the bases of angiospermous trees. Costate leaves, catenulate when dry, characterize *Claopodium* but *Iwatsukiella* has neither of those features.

Jaffueliobryum* Thériot, 1928. see *Grimmia

- Jaffueliobryum raui* (Austin) Thériot
- Jaffueliobryum wrightii* Sullivant in Sullivant & Lesquereux

Two genera, *Jaffueliobryum* and *Coscinodon*, have been removed from *Grimmia* on the basis of the very distinctive calyptra: campanulate, plicate, fringed basally. The uninitiated person viewing that feature might even think of the unrelated genus, *Orthotrichum*. *Coscinodon* has exserted capsules; *Jaffueliobryum* has immersed capsules. *Jaffueliobryum* is a genus of mosses occupying rocks in our southeastern deserts. One is alerted in such areas to think of *Jaffueliobryum* when one sees an ashy brown or tan moss with very long and decurrent hyaline awns. In the field, our two species of *Jaffueliobryum* approach *Crossidium* because of the dense and erect awns on the dry plant.

***Kiaeria* I. Hagen, 1915.**

The plants in the following key are small and erect with falcate leaves and with the costa excurrent in a narrowly subulate apex. The leaf margin is entire to faintly serrulate and the costa is without stereid bands.

Species included in this key: all Dicranaceae, except *Blindia* (Seligeriaceae)

- Arctoa hyperborea* (Withering) Bruch & W. P. Schimper*
- Arctoa fulvella* (Dickson) Bruch & W. P. Schimper
- Blindia acuta* (Hedwig) Bruch & W. P. Schimper
- Kiaeria blyttii* (Bruch & W. P. Schimper) Brotherus
- Kiaeria falcata* (Hedwig) I. Hagen
- Kiaeria starkei* (Weber & D. Mohr) I. Hagen

Kiaeria differs from the closely related *Arctoa* primarily in capsule morphology. *Kiaeria* has a somewhat inclined and asymmetric capsule with a small struma; *Arctoa* has an erect, non-strumose capsule that is sulcate and strangulate when old and deoperculate. Both are plants of montane and alpine rocks in the north of the state. Both are autoicous and usually with sporophytes. Identification of *Kiaeria* depends strongly on the placement of the perigonia. If one has perichaetial or sporophytic material, a search of leaf axils very near the perichaetium should reveal the perigonia in *K. falcata* and *K. starkei*. Failure to find such perigonia signals the probability of *K. blyttii*, a species typically with perigonia on the apex of a separate small branch.

In keeping with the gametophyte emphasis of this work, we have used leaf characters, particularly alar features, but we use them while issuing a strong caveat. The majority of examples of *Kiaeria* are placed easily, but a large minority seem to exhibit intermediate features.

- A. Auricle present and formed of thin-walled, brownish cells that are often left on stem with careless dissection; marginal cells narrowly rectangular to linear; median laminal cells 6–10:1. *Blindia acuta*
- A. Leaves with a non-auriculate base but with alar region more less distinct; marginal cells of median lamina short rectangular with the interior laminal cells seldom more than 5:1. B
- B. Capsule strongly ribbed when dry, erect, not strumose, with exothecial cells short and thick-walled. C
- B. Capsule not, or lightly, sulcate, inclined and strumose with exothecial cells various. D
- C. Laminal cells above the leaf middle mostly 1–2:1; leaves 3–5 mm long; peristome teeth erect when dry. *Arctoa hyperborea**
- C. Laminal cells above leaf middle rectangular, 2–5:1; leaves 2–3 mm long; peristome teeth when dry widely spreading from mouth of capsule. *Arctoa fulvella*
- D. Cells of alar region sharply demarcated, somewhat inflated; perigonium mostly within a few cells of perichaetium; exothecial cells more than 4:1 with lumen wall ratio about 5–8:1. *Kiaeria starkei*
- D. Cells of alar region not very inflated with only a gradual transition toward the median laminal region; perigonium and exothecial cells various. E
- E. Leaves somewhat distorted to almost crispate when dry; perigonia either near base of perichaetial stem or on a separate branch; capsule not at all sulcate; exothecial cells more than 4:1 with lumen wall ratio about 5–8:1. *Kiaeria blyttii*
- E. Leaves falcate but not at all distorted when dry; perigonium mostly within a few cells of perichaetium; capsule often very lightly sulcate when old and deoperculate; exothecial cells less than 2:1 with lumen/wall ratio less than 4:1. *Kiaeria falcata*

Kindbergia* Ochyra, 1982. see also *Hylocomium

The mosses in this section are plumosely branched pleurocarps with the branch axes somewhat arched above the substratum. The stem leaves are markedly broader and more spreading than the patent branch leaves. The stem leaves are usually very lightly plicate with the plicae restricted to the immediate base.

Species included in this key: all Brachytheciaceae

- Kindbergia oregana* (Sullivant) Ochyra
- Kindbergia praelonga* (Hedwig) Ochyra

The genus *Kindbergia* is the product of one of many only partially successful attempts to break up a too-diverse genus, *Eurhynchium*. The genus is quite distinctive in all of North America but it blends almost imperceptibly into *Eurhynchium* in much of Eurasia. In western North America, the genus *Kindbergia* is easily recognized by the combination of planar or somewhat planar branching; leaves costate to near the apex; branch and stem leaf differentiation with the latter strongly reflexed from stem and markedly decurrent. Our two species are best differentiated by habitat preferences. *Kindbergia oregana* occupies mesic, shaded to partially shaded, often alluvial sites mostly on flat ground over leaf litter; *K. praelonga* occupies rather heavily shaded sites along rivers, especially in splash zones of cascading streams.

- A. Plant regularly plumose with a single main stem from which arises shorter, nearly unbranched, lateral stems; plant mainly of coastal moderately low elevation sites. *Kindbergia oregana*
- A. Plant irregularly branched or tri- to tetra-pinnate; plant mainly of higher elevation, or of deeply shaded sites. *Kindbergia praelonga*

Leptobryum* (W. P. Schimper in Bruch & W. P. Schimper) Wilson, 1855. see *Meesia
Leptobryum pyriforme (Hedwig) Wilson

Leptobryum pyriforme is easily recognized by the very long and narrow, crispate to flexuose leaves with a costa that broadens near the base and fills about 1/3 of the leaf base. It is a common plant on moist soil banks, seeps and springs away from the humid northwest coast of California. The pyriform, inclined capsules are almost always present and highly diagnostic.

Leptobryum has for years been considered a member of the Bryaceae but recent work has transferred it to the small family Meesiaceae. This latter family has a cryptic feature which distinguishes its members from all other bryophytes. Every bryophyte has "axillary hairs," filamentous structures which arise from the immediate leaf axils. These hairs are typically so fugaceous that one may not be able to find them on leafy stems from older parts of the plant. When young stems very near the growing apex are denuded of leaves these filamentous structures are normally found. One may find taxonomically useful observations of the length of the hairs and the number of constituent cells. The cells of the axillary hairs may be uniform throughout but more commonly the immediate basal cell may be different in shape and coloration from the remaining cells of that hair. Sometimes, also, the most distal cell of the hair may be differentiated. The Meesiaceae are unique among mosses in having strongly persistent axillary hairs with several basal cells strongly reddened.

Leptodictyum* (W. P. Schimper) Warnstorf, 1906. see *Amblystegium*, *Drepanocladus
Leptodictyum humile (Palisot de Beauvois) Ochyra
Leptodictyum riparium (Hedwig) Warnstorf

Leptodictyum is an aquatic or semi-aquatic pleurocarp with small and quadrate alar cells, with lanceolate leaves whose margins are plane and entire or nearly so. The costa of *Leptodictyum* ends many cells before the leaf apex, and the median laminal cells may be rather short prosenchymatous. Basically, *Leptodictyum* has the areolation of an *Amblystegium* but the latter is a smaller plant often of mesic sites. *Leptodictyum* differs from the aquatic *Hygroamblystegium* in that the species in the latter genus have very broad costae.

Leptophascum* J. Guerra & M. J. Cano, 1989. see *Tortula
Leptophascum leptophyllum (C. Müller Hal.) J. Guerra & M. J. Cano

Leptophascum is exclusively a plant of disturbed soil, especially soil in urban areas that becomes wet from seepage or dripping. It is unique among local mosses in having smooth laminal cells but marginal cells that are unipapillose and give that margin a crenulate appearance. Until very recently *Leptophascum leptophyllum* was placed in the genus *Chenia* Zander.

Leptopterigynandrum* C. Müller Hal., 1897. see *Lescuraea
Leptopterigynandrum austro-alpinum C. Müller Hal.
Leptopterigynandrum is a very discontinuously distributed plant with a range extending from Alaska

to Argentina in montane and alpine regions. Tentative identification can be suggested by the small plants with somewhat julaceous stems whose leaves have a strongly forked costa. Compound microscope views are necessary to confirm the identification as one looks for the minutely verruculose cuticle on the branch and stem leaves.

***Lescuraea* Bruch & W. P. Schimper, 1851.**

Mosses treated in this section are pleurocarpous, often julaceous mosses with elliptic to short rectangular, rather thick-walled cells and mostly with a large group of thick-walled quadrate cells. All these plants are prostrate on the substratum, and this separates them from the plants with similar leaf areolation treated in this paper under *Antitrichia*. Many of the plants treated here have leaf-like paraphyllia obvious on the surface of the denuded stem. Most of the plants treated here have papillose median cells, some species with those papillae over the lumen center and some over the distal ends of the cells.

Species included in this key: all Leskeaceae except *Iwatsukiella* and *Pterigynandrum* (Pterigynandraceae) and *Tripterocladium* (Hypnaceae)

- Iwatsukiella leucotricha* (Mitten) W. R. Buck & H. Crum*
- Leptopterigynandrum austro-alpinum* C. Müller Hal.
- Lescuraea atricha* (Kindberg in Macoun & Kindberg) E. Lawton
- Lescuraea baileyi* (Best & Grout in Grout) E. Lawton*
- Lescuraea incurvata* (Hedwig) E. Lawton
- Lescuraea pallida* (Best) Norris & Shevock
- Lescuraea patens* (Lindberg) Arnott & C. E. O. Jensen
- Lescuraea radicata* (Mitten) Mönkemeyer
- Lescuraea saviana* (De Notaris) E. Lawton
- Lescuraea stenophylla* (Renauld & Cardot) Lindberg
- Leskea polycarpa* Ehrhart ex Hedwig
- Pseudoleskeella serpentiniensis* P. Wilson & Norris
- Pterigynandrum filiforme* Hedwig
- Tripterocladium leucocladulum* (C. Müller Hal.) A. Jaeger

All our species of *Lescuraea* are treated in the majority of recent works as a separate genus, *Pseudoleskea*. We are decidedly unconvinced that mere reduction of the peristome (*Lescuraea*) is adequate basis for separating a taxon from plants with a typical Hypnobryalean peristome (*Pseudoleskea*). Our species of *Lescuraea*, in our broadened sense, grow primarily on seasonally moist rock outcrops and boulders in montane regions. *Lescuraea stenophylla* is, however, primarily an epiphyte especially regular on the limbs of *Alnus* in areas where it is weighted down to the ground by the heavy snows of winter.

- A. Costa weak, usually ending at or before mid-leaf, often distally forked; plant typically at least somewhat julaceous. B
- A. Costa stronger, extending to or beyond the base of the acumen. F
- B. Leaves with a hyaline awn; plant of foggy mountain ridges in northwestern Oregon. *Iwatsukiella leucotricha**
- B. Leaves without such an awn. C
- C. Paraphyllia present, foliose to variously lobed; median leaf cells prorate at both ends on dorsal leaf surface; costa absent or short and double; plants mostly rather irregularly branched. *Pterigynandrum filiforme*
- C. Paraphyllia absent; costa extending to near mid-leaf, sometimes forked; median leaf cells smooth or obscurely papillose; plants closely pinnately branched. D
- D. Leaf cells with cuticular verruculoseities (view under high magnification and low light intensity); costa distally forked; leaves somewhat falcate. *Leptopterigynandrum austro-alpinum*
- D. Leaf cells smooth; costa forked or not; leaves mostly symmetric. E
- E. Plants mostly with a russet to reddish blush; costa broad and flattened, forked distally; median and more distal cells of leaf seldom more than 3:1. *Pseudoleskeella serpentiniensis*
- E. Plant green to brownish; costa slender, not forked distally; median and more distal cells of leaf at least in part more than 4:1. *Tripterocladium leucocladulum*
- F. Cells strongly unipapillose over the center of the lumen. G
- F. Cells smooth or with low papillae over the cell ends. H
- G. Leaf margins strongly recurved from base to middle of leaf or beyond; some cells in the leaf middle 2:1. *Lescuraea patens*
- G. Leaf margins plane or recurved only near the base; all median cells isodiametric. *Leskea polycarpa*

- H. Paraphyllia absent; juxtacostal cells of leaf base longer than the median cells. *Lescuraea baileyi**
 H. Paraphyllia present, easily seen on stems and branches after removal of leaves. I
 I. Base of acumen of branch leaves with a recurvature that specially separates that acumen from the rest of the leaf. J
 I. Leaf margin recurved primarily at the base with acumen not so defined. K
 J. Leaves gradually narrowed to a long acumen that nearly equals or exceeds the length of the rest of the leaf; leaves mostly straight and symmetric; plant mostly corticolous in alder groves at high elevations. *Lescuraea stenophylla*
 J. Leaves with the acumen shorter; leaves somewhat falcate by reason of the obliquely oriented acumen; plant epipetric. *Lescuraea saviana*
 K. All cells of the acumen shorter than 4:1; walls of median cells mostly with lumen:wall ratio less than 3:1. L
 K. At least some cells in acumen more than 4:1; lumen:wall ratio of median cells more than 5:1. M
 L. Median cells of stem leaves, sometimes also of branch leaves pitted; all alar cells quadrate to short rectangular. *Lescuraea atricha*
 L. Median cells of stem leaves not pitted; some of the alar cells transversely elongate. *Lescuraea incurvata*
 M. Leaves quite strongly concave; branches ascending to erect; cells pellucid and somewhat bulging; plant of high mountain sites in the Sierra and Cascades. *Lescuraea pallida*
 M. Leaves not strongly concave; stems and branches mostly prostrate to decumbent; cells rather opaque; plant of montane sites in the Klamath Range. *Lescuraea radicata*

Leskea* Hedwig, 1801. see *Lescuraea

Leskea polycarpa Ehrhart ex Hedwig

The classical distinction between *Leskea* and *Lescuraea* centers upon the autoicous sexuality of *Leskea* and the dioicous sexuality of *Lescuraea*. It is of some interest that most of our species of *Lescuraea* often produce sporophytes while our only *Leskea* (*L. polycarpa*) has not yet been seen with sporophytes in California. The description of a plant as "dioicous" must be done with great care, and reports of such must be read with caution. *Leskea polycarpa* closely resembles *Lescuraea patens* and is best recognized by the greener coloration of the former and the brownish wash of the latter.

Leucolepis* Lindberg, 1868. see *Plagiomnium

Leucolepis acanthoneura (Schwägrichen) Lindberg

Leucolepis is one of the most easily recognized of mosses. The plant is truly dendroid (as opposed to plumose), and it thus may resemble a palm (an erect stem that distally has a clustered series of spirally inserted branches). The only other western North American plants that can be considered truly dendroid are *Climacium* (not yet found in California) and *Thamnobryum* (rarely encountered in mixed conifer forests in northern California). *Climacium* can be readily recognized by the dense coating of paraphyllia-like structures over the stems and branches (visible even under a hand-lens). *Thamnobryum* has broadly rounded leaf apices differing from the acute to acuminate apices of *Leucolepis*. The deltoid triangular leaves on the erect main stem of *Leucolepis* differ from the stem leaves of the other two dendroid genera both in their shape and in the bleached nature of those leaves even in the young plant.

Limbella* (Brotherus) Brotherus, 1927. see *Amblystegium

Limbella fryei (R. S. Williams) Ochrya*

Limbella is easily recognized as a fairly large pleurocarpous moss with the long lanceolate leaves bordered by a limbidium of elongate and thick-walled cells. It is now known from a single wetland site in coastal Oregon. *Limbella tricostata*, the sister species to *L. fryei*, is an Hawaiian endemic.

Lorentziella* C. Müller Hal., 1879. see *Acaulon

Lorentziella imbricata (Mitten) Brotherus

Only two California mosses have spores large enough to be seen with the naked eye (100 μ m). These are *Lorentziella* that, appropriately enough, belongs to the family Gigaspermaceae (giant spores), and *Archidium*. Both these plants appear to be ephemerals of barren soil in winter and early spring, and they

Meteorium is the type genus of the family Meteoriaceae, a group of mosses largely restricted to the tropics and to the Southern Hemisphere. It is basically a group of epiphytic Brachytheciaceae-like mosses with papillosity and with large auriculate leaf bases. *Meteorium nigrescens* has been found in Baja California but it is so far unknown from California. Were it to be found, it would probably be recognized as a pleurocarpous moss whose spreading leaves are discolored almost jet-black on the older stems.

Microbryum W. P. Schimper, 1860.

Mosses included in this section are very small bulbiform acrocarps growing in winter and early spring on seasonally moist and sunny soil. They have erect and exserted sporophytes with elliptic to short cylindric capsules, and the leaves are papillose.

- Species included in this key: all Pottiaceae
- Microbryum davallianum* (J. E. Smith) Zander
 - Microbryum starckeanum* (Hedwig) Zander
 - Microbryum vlassovii* (Lazarenko) Zander*

Traditional classifications of the family Pottiaceae placed in the genus *Pottia* nearly all the very small and largely ephemeral plants with broad leaves and a single abaxial stereid band in the costa. Zander (1993) presents a strong case for a reduction of the size of the genus with many of the previously included members now viewed as members of *Tortula*. That realignment means that the type of *Pottia* is now in *Tortula*, and so, a new name is required.

The species of *Microbryum* are among the smallest of the mosses in the Pottiaceae, and they are unlikely to be collected except when sporophytes are present. The peristome of the various species of *Microbryum* is absent or very much reduced usually to truncate stubs. The spores of *Microbryum* are typically more than 20 µm in diameter, and they are usually strongly papillose to warty-papillose. Even when sterile, *Microbryum* can be recognized by the very bulbiform plants with each leaf ending in a short and colored mucro. Such plants should be tested with a drop of 10% KOH for the very red coloration that is immediately visible upon application. Under the compound microscope the poor demarcation of the alar region of *Microbryum* sets it apart from most of *Tortula*.

- A. Costa and adjacent lamina with distal portion covered on adaxial side with a cushion of bottle-shaped and papillose cells; capsule immersed to slightly emergent, cleistocarpous on a short seta. *Microbryum vlassovii**
- A. Costa without such an adaxial cushion; capsule exserted. B
- B. Leaves mostly more than 2:1, with a reddish apiculus; spores densely spinulose. *Microbryum davallianum*
- B. Leaves mostly less than 2:1, with a short yellowish apiculus; spores finely papillose. *Microbryum starckeanum*

Mielichhoferia Nees & Hornschuch, 1831. see *Pohlia*

Mosses considered in this section produce clones that are strikingly glaucous with a distinctive and unique blue-green coloration. They typically cover extensive, yet highly localized, areas on highway roadcuts, and these clones have the peculiar feature of growing as contiguous plants that are on inspection a close association of many individual tufts each of differing heights. The rather large pale green sporophytes are often present in the colony despite their putatively dioicous nature.

- Species included in this key: all Mielichhoferiaceae
- Mielichhoferia elongata* (Hoppe & Hornschuch ex W. J. Hooker) Nees & Hornschuch in Nees
 - Mielichhoferia tehamensis* Showers
 - Schizymenium shevockii* A. J. Shaw

Members of the genus *Mielichhoferia* should be easily assigned to alliance with *Pohlia* (Mniaceae) on the basis of the acrocarpous habit, the rather large but elongate cells with some of the distal cells of the leaf sparingly prorate, and the papillose rhizoids. The peculiar growth habit of these mosses is markedly different from that of *Pohlia*. First, unlike the mostly soil-inhabiting *Pohlia*, our species of *Mielichhoferia* and *Schizymenium* are generally petricolous.

Most of our collections of *Mielichhoferia elongata* come from seasonally wet metamorphic rocks, mostly ones with a high concentration of heavy metal ores, especially copper. It is often there associated with *Schizymenium shevockii*. *Mielichhoferia tehamensis* seems to be restricted to the volcanic rocks in alpine areas in the Mount Lassen region. Based on preliminary analysis by Spence (personal communication), it is likely that *Mielichhoferia tehamensis* will be transferred to a different genus and family,

- A. Leaves recurved at least near their bases. *Mielichhoferia elongata*
- A. Leaf margins plane throughout. B
- B. Median leaf cells to 15 µm wide; leaves erect spreading, acute to acuminate distally; peristome present. *Schizymenium shevockii*

- B. Median leaf cells to 10 μm wide; leaves erect, often rigidly so, obtuse distally; peristome absent.
..... *Mielichhoferia tehamensis*

***Mnium* Hedwig, 1801.**

Mosses included in this key are acrocarps with broad leaves, isodiametric to shortly elliptical smooth cells, and with a geminate-toothed limbidium. Such a moss could be confused with *Atrichum* but that genus has photosynthetic lamellae along the abaxial surface of the costa.

Species included in this key: all Mniaceae

- Mnium ambiguum* H. L. H. Müller*
- Mnium arizonicum* Amann
- Mnium blyttii* Bruch & W. P. Schimper
- Mnium marginatum* (Withering) Palisot de Beauvois
- Mnium spinulosum* Bruch & W. P. Schimper
- Mnium thomsonii* W. P. Schimper

Several untraditional characters are emphasized in *Mnium*. We speak of “corner thickenings” as areas of thickened cell walls at the intersection of three adjacent cells. In such an area, the corner thickening is visible as a triangular area of wall material. Corner thickening is more frequently emphasized in liverworts where the word “trigone” is used.

Many bryophytes have teeth on the abaxial face of the distal portion of the costa. Such teeth are best seen by turning an excised leaf so that the abaxial face is in view. Focusing up and down on that costa should reveal any teeth that may be present. Sometimes abaxial teeth are even more clearly seen when an entire leafy branch is mounted on the slide. Under such conditions one may be able to see a leaf in profile with the teeth protruding out from the costa.

Mnium blyttii may be difficult to place in *Mnium* because its marginal teeth are often abortive or wanting. Lacking such teeth, one might place it in *Rhizomnium*, and we have placed it in that key as well.

- A. Leaf margins mostly entire or with a few poorly developed teeth, only occasionally with those teeth geminate; plant with a post-mortal reddish blush; limbidium 1–2 cells wide and 1–2 cells thick; costa not confluent with limbidium. *Mnium blyttii*
- A. Leaf margins prominently geminate from at least mid-leaf to apex; plant without a post-mortal reddish blush; limbidium mostly wider and thicker; costa length variable. B
- B. Cells with somewhat angular lumina due to the equal thickening of the cell walls. C
- B. Cells with more or less rounded or elliptic lumina due to the trigone-like corner thickenings. ... E
- C. Leaf cells elongate in radiating rows from costa to margin; marginal teeth often inconspicuous.
..... *Mnium arizonicum*
- C. Leaf cells not in radiating rows or the rows parallel to the costa; marginal teeth conspicuous. ... D
- D. Costa confluent with limbidium at apex. *Mnium spinulosum*
- D. Costa ending before apex. *Mnium thomsonii*
- E. Median leaf cells mostly more than 20 μm in diameter; costa seldom with abaxial teeth; many leaves long acuminate at apex; marginal teeth blunt. *Mnium marginatum*
- E. Median leaf cells mostly less than 20 μm in diameter; costa with abaxial teeth; leaves short acute at apex; marginal teeth sharply acute. *Mnium ambiguum**

Molendoa* Lindberg, 1878. see *Gymnostomum

Molendoa sendtneriana (Bruch & W. P. Schimper) Limpricht

Molendoa is a rare moss in California perhaps best distinguished from *Gymnostomum* by the tendency to have tristichous leaves with papillae more centrally located over the cell lumina thus giving the cells a more pellucid look.

Myurella* Bruch & W. P. Schimper, 1853. see *Heterocladium

Myurella julacea (Schwägrichen) Bruch & W. P. Schimper

Myurella is one of the smallest pleurocarpous mosses in California. It can be recognized as a glaucous moss with julaceous stems and branches. It seems to be confined to recesses in rock outcrops in alpine and subalpine areas.

Neckera Hedwig, 1801.

The plants treated here are either truly dendroid mosses (see discussion under *Antitrichia*), or they are plumose mosses with complanate leaf arrangement. The monotypic genus *Bestia* is here treated despite its plumose branching and more or less julaceous leaf arrangement. Because the circumscription of the Neckeraceae remains in some uncertainty, *Bestia* has shuffled between the Neckeraceae and the Brachytheciaceae.

Species included in this key: all Neckeraceae except *Bestia* (Brachytheciaceae); *Climacium* (Climaciaceae); and *Leucolepis* (Mniaceae)

- Bestia longipes* (Sullivant & Lesquereux) Brotherus
- Bryolawtonia vancouveriensis* (Kindberg) Norris & Enroth
- Climacium dendroides* (Hedwig) Weber & D. Mohr*
- Homalia trichomanoides* (Hedwig) W. P. Schimper*
- Leucolepis acanthoneura* (Schwägrichen) Lindberg
- Metaneckera menziesii* (Drummond) W. C. Steere
- Neckera douglasii* W. J. Hooker
- Porotrichum bigelovii* (Sullivant) Kindberg
- Thamnobryum neckeroides* (W. J. Hooker) E. Lawton

Most of the plants in this key are easily identified. Students may sometimes confuse the expressions “complanate-foliate” and “planar branched.” Planar branching is a feature of the branching independent of the apparent flat arrangement of the leaves. Many mosses with complanate leaves may be prostrate on the substratum with the branching therefore appearing planar, but the plumose plants here in the Neckeraceae key have the branches lifted somewhat off the substratum with those branches remaining in a single plane.

- A. Leaves complanate; plant not dendroid but sometimes irregularly plumose. B
- A. Leaves not complanate; plant mostly dendroid to plumose. F
- B. Leaves strongly undulate. C
- B. Leaves not at all undulate. D
- C. Leaves ecostate; leaf apex acute to acuminate, strongly dentate, mostly with some of the teeth recurved in the plane of the leaf; paraphyllia absent. *Neckera douglasii*
- C. Leaves with strong costa reaching above mid-leaf; leaf apices blunt to obtuse, serrulate to nearly entire; paraphyllia densely arranged on main stems and branches. *Metaneckera menziesii*
- D. Juxtacostal cells in median leaf 4–8:1; leaves usually more than 1.5 mm long; margin of most leaves broadly recurved near the base on one side. *Porotrichum bigelovii*
- D. Juxtacostal median cells shorter; not much longer than median marginal cells; leaves shorter. E
- E. Leaves to 1 mm long; alar cells quadrate in a small but poorly defined group.
 - *Bryolawtonia vancouveriensis*
- E. Leaves larger; alar cells not at all differentiated. *Homalia trichomanoides**
- F. Leaf margin with somewhat elongate cells forming a somewhat differentiated limbidium; leaves of stem bleached and deltoid-triangular, markedly different from those of the branches.
 - *Leucolepis acanthoneura*
- F. Leaf margin without a limbidium; stem leaves not so different from those of branches. G
- G. Paraphyllia arranged in parallel lines along stems and branches; distal portion of costa without abaxial spines or cristae. *Climacium dendroides**
- G. Paraphyllia absent; distal portion of costa with abaxial spines or cristae. H
- H. Leaf apices obtuse and coarsely dentate; alar cells irregularly quadrate to rectangular, not well differentiated; leaves not plicate or recurved. *Thamnobryum neckeroides*
- H. Leaf apices mostly acute; alar cells markedly greener than adjacent laminal cells, quadrate and thick-walled with rounded lumina; leaves somewhat plicate and recurved near base.
 - *Bestia longipes*

Oedipodium Schwägrichen, 1823. see Tayloria

Oedipodium griffithianum (Dickson) Schwägrichen*

This high montane or alpine species has not yet been found south of northwest Washington State. Traditionally, it has been placed in the dung moss family (Splachnaceae) probably on the basis of the very long hypophysis on the erect capsule, and on the basis of the very spatulate leaves with large and thin-walled cells. Recent DNA sequence data suggests instead that it should be placed in the very distantly

related Polytrichopsida. Were *Oedipodium* to be encountered in California it would be found on thin soil in deep recesses in alpine rock outcrops. The very broadly spatulate leaves with long cilia on the basal margins render this moss absolutely recognizable in the field.

Oligotrichum* Lamarck & A. P. de Candolle, 1805. see *Atrichum

- Oligotrichum aligerum* Mitten*
- Oligotrichum hercynicum* (Hedwig) Lamarck & A. P. de Candolle*
- Oligotrichum parallelum* (Mitten) Kindberg*

Three members of this genus grow on wet soil banks through much of Oregon and more northern regions; and *Oligotrichum aligerum* can even be found in southern Mexico. Peculiarly, none of these species has yet been encountered in California. The combination of the leaves crispate and with photosynthetic lamellae will recall *Atrichum* and especially *Pogonatum contortum*. *Oligotrichum* differs from the former in having elimbate leaves, and it differs from the latter in being markedly smaller (less than 5 cm tall). It is easily distinguished from *Pogonatum contortum* in that the latter will never have abaxial teeth on the laminal surface, nor will it have a wavy appearance to the adaxial lamellae (in adaxial, macroscopic view).

***Oncophorus* (Bridel) Bridel, 1826.**

Mosses included in this section are acrocarpous, costate plants with the leaf bases well demarcated, closely appressed to, or sheathing, the stem, but with the leaf limb spreading, crispate when dry. The margin of the differentiated limb is bistratose in a 1–2 cell wide band, dentate and often somewhat geminate on that margin. In California, both species of *Oncophorus* usually have sporophytes. The strongly strumose capsules will allow easy identification.

Species included in this key: all Dicranaceae

- Oncophorus virens* (Hedwig) Bridel
- Oncophorus wahlenbergii* Bridel

Oncophorus is a moss of high elevation streamside and meadow situations. It typically grows best on silt-covered logs, although it may also extend out onto the adjacent soil of the streamside. It is the only acrocarpous moss with crispate and dentate leaves abruptly contracted from a sheathing base, and with smooth and isodiametric median laminal cells.

- A. Leaf broadest near the distal end of the clasping base; margin plane to ascending; apex mostly subulate, bluntly acute. *Oncophorus wahlenbergii*
- A. Leaf base with more or less parallel sides; margins recurved; leaf apex bluntly obtuse on many leaves. *Oncophorus virens*

Orthodicranum* (Bruch & W. P. Schimper) Loeske, 1910. see *Dicranum

- Orthodicranum tauricum* (Sapehin) Smirnova

Our species of *Orthodicranum* will be among the easiest to identify of California mosses. Any emerald-green acrocarpous plant with subulate leaves growing in dense wefts on logs or on tree trunks (primarily coniferous) should be examined for a pattern of regular breaking of leaf tips. *Orthodicranum tauricum* commonly accompanies *Aulacomnium androgynum* and *Dicranoweisia cirrata* on logs and tree trunks. The dispersal of the leaf tip fragments may function as a primary means of asexual reproduction in our species of *Orthodicranum*.

***Orthodontium* Schwägrichen, 1827.**

Mosses included in this section are relatively small acrocarps with very narrow leaves but with the cells of the mid-leaf thin-walled. The leaves may be somewhat distorted when dry but they are not truly crispate. The leaf margin is plane to somewhat recurved, and it is nearly entire except at the extreme apex.

Species included in this key: all Orthodontiaceae

- Orthodontium gracile* Schwägrichen ex Bruch & W. P. Schimper
- Orthodontium pellucens* (W. J. Hooker) Bruch & W. P. Schimper in C. Müller Hal.

Orthodontium has been traditionally placed in the family Bryaceae. Recent DNA sequence data suggests

that it is best viewed as a member of a separate family. It will probably be identified in the field as a Dicranaceae by an uninitiated worker. The erect and unbranched stems have leaves that appear under the hand-lens to have laminal cells too long and too small to be a Bryaceae. Even with a hand-lens, however, one would be able to see the enlarged alar cells characteristic of *Dicranum*. Without enlarged alar cells, one might think of such members of the Dicranaceae as *Dicranella* but the almost exclusively epiphytic and log habitat of *Orthodontium* should then allow easy elimination of those epipetric and episolic Dicranaceae. In California, *Orthodontium* is apparently restricted to the perhumid forests near the Pacific Coast, generally among the coastal *Sequoia*.

- A. Leaves narrowed from base to apex; costa cross-section with stereids; antheridia placed only a few leaf axils below the perichaetium; exostome teeth evenly tapering from a broad base closely striate with a zig-zag median commissural line. *Orthodontium gracile*
- A. Leaves broadest near the middle; costa cross-section with stereids; antheridia on a short branch near the base of the perichaetial stem; exostome teeth widely separated, bluntly linear and lightly papillose without a median commissural line. *Orthodontium pellucens*

Orthothecium* W. P. Schimper in Bruch & W. P. Schimper, 1852. see *Hypnum

Orthothecium chryseum (Schwägrichen in Schultes) W. P. Schimper in Bruch & W. P. Schimper*
Orthothecium chryseum is a plant primarily found in bogs and fens. No other local ecostate and pleurocarpous moss is so strongly plicate. It has not yet been found in California but should be looked for in rich fens.

***Orthotrichum* Hedwig, 1801.**

The plants included in this section are easily recognized by their sporophytes and associated structures: calyptra often hairy and plicate, capsule immersed or exserted on a short seta; capsule often sulcate and strangulate. Almost all species of *Orthotrichum* and *Ulota* are autoicous, and they are usually with sporophytes at any time of collection.

Species included in this key: all Orthotrichaceae

- Orthotrichum affine* Bridel
- Orthotrichum alpestre* Hornschuch in Bruch & W. P. Schimper
- Orthotrichum anomalum* Hedwig*
- Orthotrichum bolanderi* Sullivant
- Orthotrichum consimile* Mitten
- Orthotrichum cupulatum* Bridel
- Orthotrichum diaphanum* Schrader ex Bridel
- Orthotrichum euryphyllum* Venturi
- Orthotrichum flowersii* Vitt
- Orthotrichum hallii* Sullivant & Lesquereux
- Orthotrichum holzingeri* Renauld & Cardot in Holzinger
- Orthotrichum laevigatum* J. E. Zetterstedt
- Orthotrichum lyellii* W. J. Hooker & Taylor
- Orthotrichum macounii* Austin
- Orthotrichum obtusifolium* Bridel
- Orthotrichum pallens* Bruch ex Bridel
- Orthotrichum papillosum* Hampe
- Orthotrichum pellucidum* Lindberg
- Orthotrichum praemorsum* Venturi in Röhl
- Orthotrichum pulchellum* Brunt. in J. E. Smith & Sowerby
- Orthotrichum pumilum* Swartz
- Orthotrichum pylaisii* Bridel
- Orthotrichum rivulare* Turner
- Orthotrichum rupestre* Schleicher ex Schwägrichen
- Orthotrichum shevockii* Lewinsky-Haapasaari & Norris
- Orthotrichum speciosum* Nees in Sturm
- Orthotrichum spjutii* Norris & Vitt
- Orthotrichum striatum* Hedwig
- Orthotrichum tenellum* Bruch ex Bridel
- Orthotrichum texanum* Sullivant & Lesquereux

- Orthotrichum underwoodii* F. Lara, Gariletti & Mazimpaka
- Ulota megalospora* Venturi in Röhl
- Ulota obtusiuscula* C. Müller Hal. & Kindberg in Macoun
- Ulota phyllantha* Bridel
- Zygodon rupestris* W. P. Schimper ex Lorentz

Work with *Orthotrichum* normally requires examination of the epidermal cells of the capsule (exothecial cells) as well as features of the peristome. A longitudinal section of the capsule can be placed under a cover slip on a slide and examined under the compound microscope. There will always be a few stomates, and these may be surficial (phaneroporous) or sunken in a pit surrounded by thick-walled subsidiary cells (cryptoporous). It is especially easy to see the cryptoporous stomates because the subsidiary cell complex forms what appears to be small blisters, and these can usually be sensed even with a hand-lens. It may be more difficult to see the paired and green guard cells of the phaneroporous species but they will be found with searching, especially near the base of the urn.

A number of important taxonomic features lie in hand-lens viewing of capsules. Are the exostome teeth erect, or are they curved outward and downward along the capsule mouth? This feature will be obvious with the caveat that newly deoperculate capsules will have the teeth erect before they take their proper place in a recurved position. Are there endostome segments? Here it is best to look at a newly deoperculate capsule as the fragile segments may be lost with age. Are the capsules sulcate? Here, an older capsule is best because the longitudinal ridges of a sulcate capsule may be obscured when the capsule is young. Are the capsules strangulate? The shrinking of the capsule immediately below the mouth is also a feature of the older capsule. The hairiness of the calyptra is easily seen with a hand-lens. The majority of the *Orthotrichum* species with glabrous or sparsely hairy calyptrae have cryptoporous stomates. *Orthotrichum* normally has rather short setae, and the degree of exertion of the capsule should be clearly defined. A capsule is immersed if the longer perichaetial leaves extend beyond the capsule mouth; it is emergent if the longer perichaetial leaves extend to the level of the capsule; it is exerted if the seta is longer than any of the perichaetial leaves.

- A. Leaf margins serrate with multicellular teeth; fertile plants polysetous with seta mostly more than 2 cm long. see *Ptychomitrium*
- A. Margins entire to serrulate. B
- B. Apex of leaf filiform with about 2–5 isodiametric to short-rectangular cells in a uniseriate apex. C
- B. Apex of leaf not uniseriate. D
- C. Plant stoloniferous with prostrate axes possessing abundant red-brown rhizoids; axillary gemmae absent; erect branches short, not at all hamate when dry; median leaf cells pluripapillose with papillae blunt and covering most of cell. *Ulota megalospora*
- C. Plant erect and tufted, heavily gemmiparous in leaf axils; stem apices of dry plant strongly hamate; median leaf cells pluripapillose with papillae sharp and punctiform. ... *Zygodon rupestris*
- D. Basal marginal cells quadrate to very short rectangular, abruptly differentiated in several rows from the more elongate interior basal cells; capsules exerted with a long and well-demarcated neck; stomates phaneroporous. E
- D. Basal marginal cells not so abruptly demarcated; capsules and stomates various. F
- E. Apex of upper leaves with a reddish-brown cluster of septate gemmae; plant found only within a mile or so of the ocean. *Ulota phyllantha*
- E. Apex of leaves not gemmiparous; plant more widely distributed. *Ulota obtusiuscula*
- F. Leaves with the suprabasal, perimarginal cells having high, pointed papillae inserted not on the lumen but on end and lateral walls; plant dioicous with leaf apices either very long and somewhat flexuose when dry or with that apex bluntly eroded by gemma production. G
- F. Leaves without such a papillar arrangement; plant monoicous with leaf apices not usually long and flexuose; gemma production various. H
- G. Plant usually with dense gemmae on upper lamina and costa of most of the upper leaves; leaves not long-acuminate. *Orthotrichum lyellii*
- G. Plant without gemmae; leaves usually long-acuminate, often with elongate cells in a slightly serrulate acumen. *Orthotrichum papillosum*
- H. Leaves crispate when dry; plant growing as small tufts mainly on twigs of shrub and trees in the northwest of California; capsule with cryptoporous stomates. I
- H. Leaves erect and imbricate when dry; habit and stomate position of plant various. J
- I. Exostome red. *Orthotrichum pulchellum*
- I. Exostome white. *Orthotrichum consimile*
- J. Margins incurved to plane throughout. K

- J. Margins recurved to revolute at least at the base and usually through most of the leaf. L
- K. Plant blackish; leaf lamina bistratose; growing on moderately dry rocks. *Orthotrichum bolanderi*
- K. Plant green, often with a reddish-brown cast; lamina unistratose; growing on trees in mountains often near watercourses. *Orthotrichum obtusifolium*
- L. Stomata phaneroporous; basal cells elongate and somewhat porose or with sinuose walls. . . . M
- L. Stomata cryptoporous; basal cells short-rectangular with evenly thickened walls. W
- M. Leaves smooth; peristome smooth; calyptra glabrous; very localized plant of volcanic plateaus in northeastern California and in neighboring states to the northeast. . . . *Orthotrichum holzingeri*
- M. Leaves strongly papillose; peristome minutely to high papillose; calyptra with abundant hairs. . . N
- N. Capsule smooth, shorter than 4:1. *Orthotrichum striatum*
- N. Capsule ribbed at least in upper half; capsule longer. O
- O. Peristome reduced to a few basal plates; plant glaucous due to the very high multifid papillae; adaxial face of costa covered by laminal cells in at least the distal 1/2 of leaf; spores to 11 μ m in diameter. *Orthotrichum spjutii*
- O. Peristome fully developed; plant not glaucous; adaxial face of costa with elongate cells throughout; spores markedly larger. P
- P. Endostome at least in part two cells wide, more than half as long as exostome; mostly epiphytic plants with cylindric capsules. Q
- P. Endostome mostly not present or quite abortive; mostly rupestral plants with oblong capsules. . . . R
- Q. Capsule immersed, stragulate and strongly ribbed from near the mouth to the base; exostome teeth not fenestrate. *Orthotrichum affine*
- Q. Capsule emergent, ribbed only in distal half; exostome teeth usually fenestrate. *Orthotrichum speciosum*
- R. Sporophyte immersed so that the apices of the nearest perichaetial leaves are above the mouth of the capsule. S
- R. Sporophyte emergent to exerted. T
- S. Plant growing as small, closely aggregated, tufts on rocks or trees; exostome densely papillose. *Orthotrichum texanum*
- S. Plant growing as rather large, loose mats primarily on rocks; exostome low papillose to almost smooth. *Orthotrichum rupestre*
- T. Peristome erect to spreading when dry; endostome segments essentially absent. U
- T. Peristome reflexed and often broken but with the bases still showing that reflexing; endostome segments sometimes present. V
- U. Capsule ovate to short-oblong, exerted or nearly so; exostome teeth 16 but sometimes tardily separating from an initial 8 pairs. *Orthotrichum pylaesii*
- U. Capsule cylindric, about 1/2 emergent; exostome teeth 8, even in older capsules; leaf apices acuminate to cuspidate, often bleached. *Orthotrichum praemorsum*
- V. Leaves bluntly acute to obtuse; median cells mostly rather low papillose; adaxial surface of costa above its middle showing elongate to linear, thick-walled cells. . . . *Orthotrichum laevigatum*
- V. Leaves long-acuminate to narrowly acute; median cells with papillar salients at least as high as 1/2 the cell thickness; adaxial surface of costa above its middle covered with cells like those of the adjacent lamina. *Orthotrichum macounii*
- W. Leaves terminating in a hyaline awn. *Orthotrichum diaphanum*
- W. Leaves without hyaline awn. X
- X. Plant strongly heterophyllous with the vegetative leaves blunt and ligulate but with the leaves below the perichaetium acuminate and lanceolate, markedly enlarged relative to vegetative leaves; exostome erect to somewhat spreading, densely spiculate-papillose; endostome very short. *Orthotrichum* species A
- X. Plant isophyllous without differentiation between the vegetative leaves and perichaetial leaves; peristome with exostome reflexed and papillose with endostome obvious or erect and striate with endostome very short to absent. Y
- Y. Exostome erect or spreading, with the striate ridges on the dorsal face resembling a fingerprint; endostome absent; leaves often bistratose or with bistratose streaks; plants consistently epipetric. Z
- Y. Exostome reflexed to recurved, papillose to papillose-striate but never with a fingerprint-like pattern; endostome present; leaves unistratose; most of the species epiphytic. AC
- Z. Capsule exerted and cylindrical, mostly with 8 long ribs alternating with 8 short ones. *Orthotrichum anomalum**
- Z. Capsule immersed to emergent; with 8 or 16 ribs. AA
- AA. Capsule with 16 ribs; leaves only remotely keeled, acute. *Orthotrichum cupulatum*
- AA. Capsule with 8 ribs; leaves distally keeled, obtuse to bluntly acute. AB

- AB. Leaves unistratose, stiff, ligulate with the apices incurved; papillae high and forked; plant glaucous. *Orthotrichum pellucidum*
- AB. Leaves bistratose, lanceolate and loosely appressed; papillae low, conical and not forked; plant green to dark green. *Orthotrichum hallii*
- AC. Leaf apex rounded-obtuse and often irregularly serrate; leaves smooth to inconspicuously papillose; plant of seasonally inundated rocks or tree bases. AD
- AC. Leaf apex acute to acuminate or mucronate, entire to, at most, papillose-crenulate; leaves smooth to densely papillose; plant epiphytic or occasionally epipetric on dry rocks. AE
- AD. Leaves very dark green to nearly black; median cells mostly more than 15 μm in diameter; costa terete in cross-section; plant of rocks on stream heads in exposed dry to semi-desert sites. *Orthotrichum euryphyllum*
- AD. Leaves rich dark green, sometimes black on older portions; median cells mostly to 12 μm ; costa flat in cross-section; on trees and rocks in frequently flooded areas of stream flood-plains. *Orthotrichum rivulare*
- AE. Leaf margins bistratose; capsules immersed with seta less than 0.5 mm long. *Orthotrichum shevockii*
- AE. Leaf margins unistratose or leaf lamina bistratose throughout; capsules immersed to emergent. AF
- AF. Sporophyte immersed so that the apices of the nearest perichaetial leaves are above the mouth of the capsule. AG
- AF. Sporophyte emergent to exerted. AI
- AG. Capsules sulcate throughout, short-cylindric; endostome with 16 separate segments. *Orthotrichum underwoodii*
- AG. Capsules lightly sulcate primarily toward the strangulate mouth, mostly oblong in shape; endostome with 8 segments. AG
- AH. Leaves oblong-ovate, carinate in the rounded obtuse apex, often mucronate. *Orthotrichum flowersii*
- AH. Leaves ovate-lanceolate, not at all carinate in the acute, usually apiculate apex. *Orthotrichum pumilum*
- AI. Calyptra with hairs prorate to papillose. *Orthotrichum alpestre*
- AI. Calyptra with hairs absent or smooth. AJ
- AJ. Subsidiary cells around stomates without thickened radial walls, thus with guard cells only somewhat covered by those subsidiary cells; leaves somewhat decurrent. *Orthotrichum pallens*
- AJ. Subsidiary cells with strongly thickened radial walls that obscure the outline of the guard cells below; leaves not at all decurrent. *Orthotrichum tenellum*

Oxystegus* (Limpricht) Hilpert, 1933. see *Weissia

Oxystegus tenuirostris (W. J. Hooker & Taylor) A. J. E. Smith

Oxystegus is a generic segregate from *Trichostomum* and it shares with that genus the plane-margined leaves densely pluripapillose with a strongly differentiated base of rectangular and thin-walled epapillose cells. In some respects *Oxystegus* also approaches *Tortella* in having those cells of the base rising farther along the margin than along the costa. Like most of the other genera in its group (*Weissia*, *Trichostomum*, *Timmia*) *Oxystegus* is a plant of seasonally drying soil often on exposed road banks.

Palustriella* Ochyra, 1989. see also *Drepanocladus

Palustriella commutata (Bridel) Ochyra

Palustriella falcata (Bridel) Hedenäs*

The genus *Palustriella* was erected by Ochyra (1989) to accommodate two species previously placed in the genus *Cratoneuron*. As one of the costate pleurocarpous and prostrate mosses, one thinks of the group of plants traditionally placed in either the Amblystegiaceae *sensu lato* or the Brachytheciaceae. The aquatic or semi-aquatic habit suggests the Amblystegiaceae; and the strong costa combined with the rather short laminal cells excludes all local members of the Brachytheciaceae. The Amblystegiaceae in the traditional sense has recently been broken up with most of those plants with paraphyllia placed in the new family Helodiaceae (Ochyra 1989). While the paraphyllia of *Palustriella* are usually too small and sparse to be seen in the field, the plicate and costate leaves arranged on regularly pinnate, planar-branched stems will identify most of the specimens encountered in the field. Most of our own errant field identifications in this group have involved semi-aquatic specimens of *Brachythecium frigidum* but this latter species has some of the leaves near the stem apices with laterally twisted apices.

- A. Stem leaves deltoid-triangular with a somewhat cordate base, abruptly narrowed near the leaf middle into a long acumen; alar cells forming a large group in the cordate base. *Palustriella commutata*
- A. Stem leaves lanceolate and falcate, gradually narrowed from near the base to the long acuminate apex; alar cells forming a small group to 5 cells long at margin. *Palustriella falcata**

Paraleucobryum* (Lindberg ex Limpricht) Loeske, 1907. see *Campylopus

Paraleucobryum enerve (Thedenius in C. J. Hartman) Loeske*

Paraleucobryum is a rather large acrocarpous moss with somewhat falcate-secund and subulate leaves. Our species has virtually no leaf lamina on either side of the very broad and flattened costa. In cross-section the leaf is uniformly three cell layers thick with the internal layer formed of deep green photosynthetic cells. *Paraleucobryum enerve* is primarily a Rocky Mountain species which is occasionally found on thin soils over rocks in alpine and subalpine areas of Washington State. We expect that it will eventually be found in California.

Phascum* Hedwig, 1801. see *Acaulon

Phascum cuspidatum Hedwig

Phascum cuspidatum is the only local species of the genus. It is so small that it is seldom collected without sporophytes. When sporophytes are present, only *Acaulon* offers a source of confusion. Both these genera have erect leaves that so completely enclose the sporophyte as to hide most or all of it. Numerous differences between the two genera can be noted. The costae of *Phascum* are terete and several times as thick as the adjacent lamina, and the abaxial stereid band is obvious in a cross-section. In contrast, *Acaulon* has costae that are not much thicker than the leaf laminae, and stereid cells are usually absent in a section of the median leaf. Both genera have concave leaves with recurved margins, but the recurvature of *Phascum* often extends to near the leaf apex. *Phascum* has a strongly excurrent costa that, at least distally, appears to be keeled in the dry leaf. The laminal cells of the two genera differ markedly in that *Phascum* has predominantly quadrate cells arranged in regular longitudinal rows; those of *Acaulon* are predominantly rhomboidal, and the linear arrangement of those cells is not obvious. *Phascum* is typically distinguished from *Acaulon* by the papillosity of its leaves. That is a good distinction but the uninitiated may misinterpret as papillosity the oil bodies that appear abundantly in the leaves of both genera. It is best to place an entire plant on a slide under the microscope so that the leaves can be inspected in profile thus revealing the papillae.

***Philonotis* Bridel, 1827.**

Mosses included in this section are costate acrocarps with short rectangular cells that are prorate distally or proximally. They have a dense coating of red-brown rhizoids that arise from macronematal apparatus on older portions of the stems. Most of these plants grow on very moist soil of seepages or in bogs and fens.

Species included in this key: all Bartramiaceae

- Conostomum tetragonum* (Hedwig) Lindberg
Philonotis americana (Dismier) Dismier
Philonotis caespitosa Juratzka
Philonotis calcarea (Bruch & W. P. Schimper) W. P. Schimper
Philonotis capillaris Lindberg
Philonotis fontana (Hedwig) Bridel
Philonotis marchica (Hedwig) Bridel
Philonotis muehlenbergii (Schwägrichen) Bridel
Philonotis tomentella Molendo in Lorentz
Philonotis uncinata (Schwägrichen) Bridel*
Philonotis yezoana Bescherelle & Cardot

Identification of *Philonotis* requires a view of the abaxial surface of the leaf. A whole mount of a leafy stem often serves this need. One wishes to see the prorate-papillosity from a side view on leaves seen in profile. Additionally, one should look down vertically on an excised leaf under the compound microscope. Note that the distal or proximal positioning of the prorations on *Philonotis* leaves is based upon a view from the abaxial surface.

- A. Abaxial surfaces of median leaf cells smooth or prorate on distal ends. B
- A. Abaxial surfaces of median leaf cells prorate on proximal ends or papillose over lumen. F
- B. Leaves glaucous, obviously pentastichous; costa of lower leaves ending before the apex.
..... *Conostomum tetragonum*
- B. Leaves green to pale green, unranked or obscurely pentastichous; costa of all leaves percurrent to excurrent. C
- C. Costa percurrent; perigonia broader than the diameter of the stem with perigonial leaves spreading. *Philonotis muehlenbergii*
- C. Costa excurrent by at least a few cells; perigonia various. D
- D. Leaf margins plane; costa long-excurrent with the awn on the most distal leaves about ¼ of laminal length; distal cells of lamina mostly less than 4:1. *Philonotis capillariss*
- D. Leaf margins recurved to revolute; costa excurrent but shorter; distal cells of lamina mostly longer than 4:1. E
- E. Perigonia broader than the diameter of the stem with perigonial leaves spreading; leaves mostly more than 1.5 mm long. *Philonotis marchica*
- E. Perigonia smaller than the diameter of the stem with perigonial leaves erect; leaves mostly less than 1.5 mm long. *Philonotis uncinata**
- F. Margins plane; leaves not plicate. *Philonotis caespitosa*
- F. Margins recurved at least at base; leaves lightly plicate near base. G
- G. Leaves pentastichous, inserted on stem at more than a 30° angle, twisted around stem when dry. *Philonotis americana*
- G. Leaves imbricate, not twisted. H
- H. Leaf cells with central papillae. *Philonotis yezoana*
- H. Leaf cells prorate to nearly smooth. I
- I. Leaves mostly more than 2 mm long with costa more than 250 µm wide; cells at mid-leaf near costa with lumen:wall ratio more than 4:1; perigonial bracts acute. *Philonotis calcarea*
- I. Leaves mostly less than 1.5 mm long with costa more narrow; cells at mid-leaf near costa with lumen:wall ratio less than 2.5:1; perigonial bracts obtuse or broadly acute. J
- J. Leaves ovate; costa hardly excurrent. *Philonotis fontana*
- J. Leaves narrowly lanceolate to ovate-lanceolate; costa strongly excurrent. *Philonotis tomentella*

Physcomitrella* Bruch & W. P. Schimper in Bruch & W. P. Schimper, 1849. see *Acaulon

- Physcomitrella patens* (Hedwig) Bruch & W. P. Schimper
- Physcomitrella readeri* (C. Müller Hal.) Stone & G. A. M. Scott

The genus *Physcomitrella* is one of the winter and early spring ephemeral mosses with immersed capsules. As such, *Physcomitrella* is unlikely to be collected unless it has sporophytes. The ephemeral mosses with immersed capsules are all plants of open, often disturbed soil, but our two species of *Physcomitrella* are mainly plants of mud laid bare by the retreating water of lakes and ponds. Three Funariaceae mosses of the western United States can have immersed capsules. The capsules of *Aphanorrhagma serratum* are dehiscent by means of an operculum, have collenchymatous but otherwise thin-walled exothelial cells, and the calyptra is small, mitrate and basally fringed; our two species of *Physcomitrella* have no operculum, thick-walled but not collenchymatous exothelial cells and the calyptra is small and mitrate but not fringed. *Physcomitrium immersum* has a well-defined operculum; thin-walled and hexagonal exothelial cells, and the calyptra resembles that of *Aphanorrhagma*.

***Physcomitrium* (Bridel) Bridel, 1827.**

Of the four genera of the Funariaceae with exserted capsules, *Physcomitrium* is the one that can have either immersed or exserted capsules depending on the species. We key the one member of the genus with immersed capsules (*Physcomitrium immersum*) under *Acaulon*. The four remaining species of *Physcomitrium* must instead be distinguished from those generic members of the Funariaceae with exserted capsules (*Entosthodon*, *Funaria* and *Pyramidula*). *Funaria* is easily distinguished by its inclined and mostly sulcate capsules. *Entosthodon* is distinguished by the erect capsules, mostly with a reduced endostome. *Pyramidula* has a seta that is barely emergent, and the 4-angled, very large calyptra is completely diagnostic.

Species included in this key: all Funariaceae

- Physcomitrium californicum* E. Britton
- Physcomitrium collenchymatum* Gier
- Physcomitrium hookeri* Hampe

Physcomitrium immersum Sullivant*
Physcomitrium pygmaeum T. P. James*
Physcomitrium pyriforme (Hedwig) Hampe

The genus *Physcomitrium* must be identified by a suite of characters, both gametophytic and sporophytic. A preparation of a specimen for viewing under the compound microscope must include the mounting of one of the more developed leaves. It should also include a longitudinal section of a capsule arranged so that one can view the exothecial cells and an unfragmented peristome.

- A. Capsules immersed. *Physcomitrium immersum**
- A. Capsules exerted. B
- B. Leaves without a differentiated limbidium; dry capsule broadest at the mouth, globose or nearly so; suboral cells of capsule poorly differentiated or in few rows. C
- B. Leaves with a clear limbidium at least near middle; dry capsule not flaring, pyriform to turbinate; exothecial cells at capsule mouth rectangular, mostly in more than 8 rows. E
- C. Leaves essentially entire; costa ending a few cells before leaf apex; annulus vesiculose.
. *Physcomitrium hookeri*
- C. Leaves serrulate distally; costa percurrent to excurrent; annulus of small and essentially quadrate cells. D
- D. Operculate capsule orbicular with little definition of a neck; costa ending within 2–4 cells of apex. *Physcomitrium collenchymatum*
- D. Operculate capsule pyriform with neck nearly as long as urn; costa mostly shorter.
. *Physcomitrium pygmaeum**
- E. Leaves serrulate distally; capsule erect and pyriform. *Physcomitrium pyriforme*
- E. Leaves essentially entire; capsule erect and turbinate. *Physcomitrium californicum*

Plagiobryum* Lindberg, 1863. see *Bryum

Plagiobryum zierii (Hedwig) Lindberg*

Plagiobryum is differentiated at the generic level by the pattern of a short exostome and a longer endostome. The gametophyte of *Plagiobryum* is very similar to that of *Bryum argenteum* in color and in the somewhat julaceous aspect of the leafy stem. It, however, has elongate cells throughout rather than having quadrate basal cells as in *B. argenteum*. Additionally, the latter species has a rather long awn while *Plagiobryum* is mucronate at best. In Washington State, *Plagiobryum zierii* is a rare plant in dimly lit recesses in rock outcrops at alpine elevations.

***Plagiomnium* T. Koponen, 1968.**

The plants treated in this section are acrocarpous but the dominant vegetative axes are the “plagiotropic shoots” (stolon-like stems growing prostrate and with complanate leaves). The only erect axes are those topped by the perichaetia or perigonia. We additionally treat two species lacking plagiotropic shoots (*Plagiomnium venustum* and *Leucolepis acanthoneura*). *Plagiomnium* has broadly ovate and costate leaves with a strong limbidium. The limbidium has teeth arranged singly along the margin. The cells are short hexagonal and smooth, mostly quite large.

Species included in this key: all Mniaceae

- Leucolepis acanthoneura* (Schwägrichen) Lindberg
- Plagiomnium cuspidatum* (Hedwig) T. Koponen
- Plagiomnium drummondii* (Bruch & W. P. Schimper) T. Koponen*
- Plagiomnium ellipticum* (Bridel) Iwatsuki
- Plagiomnium insigne* (Mitten) T. Koponen
- Plagiomnium medium* (Bruch & W. P. Schimper) T. Koponen
- Plagiomnium rostratum* (Schrader) T. Koponen
- Plagiomnium venustum* (Mitten) T. Koponen

Plagiomnium was formerly a part of a more encompassing genus *Mnium*. Koponen (1968) effectively justified the splitting of the genus into a number of smaller genera of which we in California are concerned primarily with *Mnium*, *Plagiomnium* and *Rhizomnium*. *Mnium* has geminate marginal teeth on the leaves; *Plagiomnium* has singly placed marginal teeth; and *Rhizomnium* lacks marginal teeth altogether. *Plagiomnium* is commonly encountered along shaded stream banks, seeps and springs, generally on soil with a high humus content.

- A. Plant dendroid; stem leaves triangular and almost echlorophyllose; costa with teeth on the abaxial surface of most of its distal portion. *Leucolepis acanthoneura*
- A. Plant not dendroid. B
- B. Marginal teeth long and very sharp; all shoots erect with the leaves spirally inserted and arranged; costa without stereids. *Plagiomnium venustum*
- B. Marginal teeth various; plagiotropic shoots essentially always present; costa with stereids. C
- C. Leaves obtuse to rounded and somewhat emarginate at apex, usually apiculate; marginal teeth blunt and extending almost to the leaf base; leaves almost without decurrencies. *Plagiomnium rostratum*
- C. Leaves acute to acuminate; marginal teeth various. D
- D. Leaves serrate in distal ½ to ¾ but entire below. E
- D. Leaves serrate to base, or with teeth reduced to essentially absent. F
- E. Median leaf cells rather thin without corner thickenings. *Plagiomnium cuspidatum*
- E. Median leaf cells thick and with obvious corner thickenings. *Plagiomnium drummondii**
- F. Laminar cells isodiametric throughout; some leaves more than 8 mm long; rhizoids found only near the base of the sexual stems. *Plagiomnium insigne*
- F. Median to juxtacostal laminar cells slightly elongate; leaves usually less than 8 mm long; rhizoids cloaking erect stems up to the perichaetium or the perigonium. G
- G. Leaves decurrent; teeth of upper margin mostly large, with width several times greater than adjacent marginal cells. *Plagiomnium medium*
- G. Leaves not decurrent; teeth throughout mostly small and blunt, little wider than adjacent marginal cells. *Plagiomnium ellipticum*

Plagiopus* Bridel, 1826. see *Anacolia*, *Bartramia

Plagiopus oederianus (Swartz) H. Crum & L. E. Anderson*

Only one species of *Plagiopus* (*P. oederianus*) is found in the world, and that species has not yet been found in California. Its occurrence in nearby areas to the north suggests that it may be encountered here. It is a plant very similar to *Bartramia pomiformis* in possessing very narrowly subulate, strongly crispate and dentate to serrate leaf margins. The leaves differ from *B. pomiformis* in being tristichous and epillose but with cuticular streaks resembling papillae running the length of the leaf. It should be looked for in moist rock crevices at medium elevations in the extreme northwestern part of the state.

***Plagiothecium* Bruch & W. P. Schimper, 1852.**

The mosses keyed here are ecostate pleurocarps mostly with a prostrate growth habit. Most have a clearly complanate leaf arrangement; those with falcate leaves or hamate stems are here keyed under Hypnaceae.

Species included in this key: all Hypnaceae, except *Plagiothecium* (Plagiotheciaceae)

- Buckiella undulata* (Hedwig) Ireland
- Dacryophyllum falcifolium* Ireland
- Herzogiella seligeri* (Bridel) Iwatsuki
- Herzogiella striatella* (Bridel) Iwatsuki
- Isopterygiopsis pulchella* (Hedwig) Iwatsuki
- Isopterygium tenerum* (Swartz) Mitten
- Plagiothecium cavifolium* (Bridel) Iwatsuki
- Plagiothecium denticulatum* (Hedwig) Bruch & W. P. Schimper
- Plagiothecium laetum* Bruch & W. P. Schimper
- Plagiothecium piliferum* (Swartz ex C. J. Hartman) Bruch & W. P. Schimper
- Pseudotaxiphyllum elegans* (Bridel) Iwatsuki
- Vesicularia vesicularis* (Schwägrichen) Brotherus

The genera included here (except *Dacryophyllum* and *Vesicularia*) have been placed by various authors in *Plagiothecium* but this is now generally viewed as the single member of the family Plagiotheciaceae with the others placed in the large family Hypnaceae. The genus *Plagiothecium* in the older, broad sense included all mosses with complanate arrangement of the ecostate leaves. The rearrangement of familial and generic placements comes from studies of branching patterns and pseudoparaphyllial morphology as well as of outer cortical morphology of the stem. As now defined, the genus *Plagiothecium* has strongly decurrent leaves, no pseudoparaphyllia, and a differentiation of a stem hyaloderm. Our species of *Plagiothecium sensu stricto* are mostly plants of humid sites of the northwestern corner of the state.

- A. Leaves strongly decurrent. B
- A. Leaves not decurrent or with decurrency formed by a group of only 1–3 cells in total. F
- B. Leaves long-acuminate. C
- B. Leaves acute to obtuse or short-acuminate. D
- C. Leaves gradually long-acuminate, closely serrate to serrulate; central basal cells thick-walled and pitted; capsule sulcate. *Herzogiella striatella*
- C. Leaves abruptly long-acuminate with the acumen variously twisted or contorted away from stem axis; acumen remotely serrulate to almost entire; median basal cells thin-walled without pitting; capsule smooth. *Plagiothecium piliferum*
- D. Decurrency broad and somewhat auriculate; cells in decurrency markedly inflated and usually 2–4:1. *Plagiothecium denticulatum*
- D. Decurrency mostly only 1–3 cells broad, narrowing to a single cell, not at all auriculate; cells in decurrency not inflated, mostly 5–10:1. E
- E. Median leaf cells mostly less than 10 μm wide; plant strongly complanate throughout. *Plagiothecium laetum*
- E. Median leaf cells mostly broader; plant julaceous or with some branches julaceous. *Plagiothecium cavifolium*
- F. Leaves mostly more than 3 mm long, lightly undulate; median leaf cells with cuticular papillosity (view under high magnification and at low light intensity). *Buckiella undulata*
- F. Leaves markedly shorter, not undulate; median leaf cells completely smooth. G
- G. Basal cells strongly pitted; leaves serrate to serrulate; capsule sulcate. H
- G. Leaves entire to serrulate; basal cells not much pitted; capsule smooth. I
- H. Leaves long-acuminate, strongly decurrent with somewhat inflated rectangular, often reddened cells. *Herzogiella striatella*
- H. Leaves acute to short acuminate, almost not at all decurrent. *Herzogiella seligeri*
- I. Leaves broadly ovate with median cells more than 12 μm broad, mostly less than 3:1; alar cells not differentiated. *Vesicularia vesicularis*
- I. Leaves lanceolate to ovate-lanceolate; median cells more narrow and relatively longer; alar cells various. J
- J. Leaves cultriform with distal one-half falcate; pseudoparaphyllia narrowly lanceolate. *Dacryophyllum falcifolium*
- J. Leaves mostly symmetric or falcate; pseudoparaphyllia absent or filamentose. K
- K. Alar cells well demarcated, quadrate to short rectangular, thin-walled and vesicular in part; pseudoparaphyllia filamentose; gemmae filamentose and papillose. *Isopterygium tenerum*
- K. Alar cells not well differentiated; pseudoparaphyllia absent; gemmae various, not papillose. L
- L. Gemmae usually present in the axils of upper leaves, these gemmae being clusters of microphyllous, caducous branchlets; margin serrulate or even slightly serrate near apex; costa often extending to $\frac{1}{3}$ of leaf. *Pseudotaxiphyllum elegans*
- L. Gemmae uncommon, fusiform, 4–6 celled; margin almost completely entire; costa very short and sometimes not at all visible. *Isopterygiopsis pulchella*

Platydictya* Berkeley, 1863. see *Amblystegium*, *Hypnum

Platydictya jungermannioides (Bridel) H. Crum

Our single species of *Platydictya* is easily recognized in the field simply by its extremely small size and its pleurocarpous growth pattern. Microscopic features useful in identification include a leaf fewer than ten cells long with those cells rather short elliptic. The leaf margin is completely entire and there is no costa, not even a short double one. One might confuse this plant under the microscope with extremely small examples of *Amblystegium serpens* or *A. juratzkanum* but these latter mosses have an obvious but short costa, and they have quadrate to rectangular cells in a well demarcated alar region.

Platyhypnidium* Fleischer, 1923. see *Eurhynchium

Platyhypnidium riparioides (Hedwig) Dixon

Platyhypnidium riparioides is an aquatic pleurocarpous moss with nearly orbicular leaves that are denticulate to dentate over the entire margin. It could be confused only with *Scleropodium* but the appropriate members of that genus have the leaves much more concave and have them arranged in a julaceous manner. Note, too, that *Platyhypnidium* has the very *Eurhynchium* leaf cell areolation with markedly smaller distal cells relative to median cells. *Scleropodium* lacks this feature, and its line of somewhat inflated cells across the leaf base is hardly a feature of *Platyhypnidium*.

Plaubelia* Bridel, 1826. see *Weissia*Plaubelia sprengelii* (Schwägrichen) Zander*

Plaubelia sprengelii is not yet recorded for California but it is not uncommon in northern Baja California. It is easily placed in the Pottiaceae on the basis of the acrocarpous plants with isodiametric cells and with some enlargement of the basal cells. It has plane to incurved margins, and would seem close to *Timmiella* on the basis of the mammillose adaxial surface of the cells. However, *Timmiella* is bistratose while *Plaubelia* is unistratose.

Pleuridium* Rabenhorst, 1848. see *Bruchia*Pleuridium acuminatum* Lindberg*Pleuridium subulatum* (Hedwig) Rabenhorst

This is a genus of about 25 species growing mostly on disturbed or seasonally dry soil in temperate portions of both hemispheres. Because of its small size, it is seldom collected without sporophytes. When fertile, the sessile and cleistocarpous, chestnut-colored capsules on tiny plants with narrowly subulate leaves allow no confusion except with *Archidium*. This latter genus has nearly spherical capsules without even a trace of a line of dehiscence; and it possesses spores that are visible even with the naked eye ($>100\text{ }\mu\text{m}$ in diameter). *Pleuridium*, in contrast, has oblong capsules with a defined apiculus; and it has much smaller spores.

In nearly all of California, *Pleuridium* is the most abundant of the ephemeral mosses; and should especially be looked for during the period from December to March.

Pleurozium* Mitten, 1869. see *Hylocomium*Pleurozium schreberi* (Bridel) Mitten*

In most northern regions including Oregon, *Pleurozium* is one of the most common mosses in a variety of habitats ranging from coastal bogs to montane forests to alpine timberline krummholz. Puzzlingly, it has not yet been found in California. It is a large plumose moss with reddish stems and with bluntly rounded leaves. The only moss that can be confused with *Pleurozium* is *Entodon concinnus* (De Notaris) Paris. This latter moss is not yet found in the area covered by this key but occurrence is a definite possibility. *Pleurozium schreberi* will surely be found in boggy sites in northern California but this finding has the potential of instead being *Entodon concinnus*. These two mosses can occupy similar habitats and so closely resemble one another as to require a cross-section through the alar region. *Pleurozium schreberi* has a unistratose alar region; *E. concinnus* has a bistratose alar region.

***Pogonatum* Palisot de Beauvois, 1804.**

In the key that appears below we treat those plants with photosynthetic lamellae so numerous as to cover nearly all the surface of the leaf lamina. The plants here treated have the terminal cell of the photosynthetic lamellae variously ornamented with papillae or cuticular ridges. The plants with numerous photosynthetic lamellae but smooth terminal cells of the lamellae are treated under *Polytrichum*.

Species included in this key: all Polytrichaceae

Meiotrichum lyallii (Mitten) G. L. S. Merrill*Pogonatum contortum* (Menzies ex Bridel) Lesquereux*Pogonatum dentatum* (Bridel) Bridel**Pogonatum urnigerum* (Hedwig) Palisot de Beauvois**Polytrichastrum alpinum* (Hedwig) G. L. Smith

Historically, the majority of the species of the family Polytrichaceae have been apportioned between the two genera *Polytrichum* (capsules longitudinally ribbed) and *Pogonatum* (capsules not at all ribbed). As such, the largely tropical and Southern Hemisphere genus, *Pogonatum*, has included *Polytrichastrum alpinum*, as well as *Pogonatum contortum* and *Pogonatum urnigerum*. Modern classification stemming in part from the work of Smith (1971) requires attention to additional largely microscopic characters of the sporophyte; and this removes *Polytrichastrum alpinum* from the genus *Pogonatum*.

At this time, we have verified records of *Pogonatum* only on the basis of *Pogonatum contortum*. *Pogonatum urnigerum* is a common plant on soil banks at high to middle montane elevations in Oregon and farther north. Surely, it will eventually be found in California. *Pogonatum contortum* is restricted to soil bank sites at low to middle elevations in the northwest corner of the state. The photosynthetic lamellae that help to define the family Polytrichaceae are obvious across almost the entire width of the distal portion of the leaf. *Pogonatum contortum* gets its name from the highly crispate nature of the leaf of the

dry plant; and, among Polytrichaceae, it shares that crispate character only with the genus *Atrichum*, a plant with only a few photosynthetic lamellae restricted in insertion to the area of the costa. Members of the genus *Oligotrichum* should be looked for in California but they have not yet been found south of Oregon.

- A. Terminal cell of each photosynthetic lamella smooth throughout; plant green and strongly crispate when dry.

A. Terminal cell of each photosynthetic lamella with obvious papillosity especially on distal end; plant glaucous, not at all crispate when dry.

B. Terminal cell of photosynthetic lamellae longer than broad with papillae on that cell rather inconspicuous.

B. Terminal cell of photosynthetic lamellae as broad or broader than long with papillae on that cell very conspicuous.

C. Excised leaf tending to turn over on its side and to describe 180 degrees of arc when laid on the slide; cells of leaf lamina across the shoulder mostly transversely elongate with transverse walls markedly thicker than lateral walls; outermost walls of terminal cell of photosynthetic lamellae almost as thick as lumen.

C. Excised leaf tending to lie flat on the slide; cells of leaf lamina across the shoulder mostly quadrate without transverse walls thickening; outermost walls of terminal cell of photosynthetic lamellae rather thin.

D. Terminal cell of photosynthetic lamellae round in section, of same size as adjacent cells of lamellae as seen in lamellar scrape; teeth of leaf margin mostly unicellular; cells hyaline and thin-walled at leaf margin at distal area of leaf base.

D. Terminal cell of photosynthetic lamellae distally flat, smaller in longitudinal diameter than adjacent non-terminal lamellar cells as seen in lamellar scrape; teeth of margin multicellular; shoulder of leaf without a hyaline border.
- Pogonatum contortum*

B

C

D

Polytrichastrum alpinum

Meiotrichum lyallii

*Pogonatum urnigerum**

*Pogonatum dentatum**

***Pohlia* Hedwig, 1801.**

Mosses treated in this section are unicostate acrocarps with capsules cylindric, often long, inclined to pendent, occasionally erect.

Species included in this key: all Mniaceae, except *Anomobryum* (Bryaceae), *Discelium* (Disceliaceae), and *Leptobryum* (Meesiaceae)

- Anomobryum julaceum* (Schrader ex P. G. Gärtner, B. Meyer & Scherbius) W. P. Schimper
- Discelium nudum* (Dickson) Bridel
- Epipterygium tozeri* (Greville) Lindberg
- Leptobryum pyriforme* (Hedwig) Wilson
- Pohlia andalusica* (Höhnelt) Brotherus
- Pohlia annotina* (Hedwig) Lindberg
- Pohlia bolanderi* (Lesquereux) Brotherus
- Pohlia camptotrachela* (Renauld & Cardot) Brotherus
- Pohlia cardotii* (Renauld) Brotherus
- Pohlia cruda* (Hedwig) Lindberg
- Pohlia drummondii* (C. Müller Hal.) Andrews in Grout
- Pohlia elongata* Hedwig
- Pohlia filum* (W. P. Schimper) Mårtensson
- Pohlia lescuriana* (Sullivant) Ochi
- Pohlia longibracteata* Brotherus in Röhl
- Pohlia ludwigii* (Sprengel ex Schwägrichen) Brotherus
- Pohlia nutans* (Hedwig) Lindberg
- Pohlia obtusifolia* (Villars ex Bridel) L. Koch
- Pohlia pacifica* A. J. Shaw
- Pohlia prolifera* (Kindberg) Brotherus
- Pohlia sphagnicola* (Bruch & W. P. Schimper) Lindberg & Arnell*
- Pohlia tundrae* A. J. Shaw
- Pohlia vexans* (Limpricht) H. Lindberg*
- Pohlia wahlenbergii* (Weber & D. Mohr) Andrews in Grout

Pohlia has until recently been classified with *Bryum* in the family Bryaceae. Research on DNA sequencing now places it in the Mniaceae. *Pohlia* differs from most species of *Bryum* in having no trace

of a limbidium and in the median cells longer than those of *Bryum*. We have since looked for characters in *Pohlia* that might suggest a Mniaceae placement. *Pohlia* differs from *Bryum* and approaches the Mniaceae in more generally having thick-walled cells in the leaf lamina. This feature is emphasized in the pattern of toothing of the leaf margins. The toothing of *Bryum* is generally formed primarily from lumen extensions with the cell walls of the teeth not significantly thickened toward the tooth apex. The toothing of *Pohlia* is, in large part, formed with extra thickening of the wall especially in the region of the tooth apex. For this feature of toothing by wall thickening, we use the prefix “crassi-” before the words serrate, dentate etc. It is important that this distinction be recognized because “crassi-serrate” cells are perfectly correlated in the Bryales with the capacity to produce prorate cells in the lamina. In this connection, it is interesting that close examination of *Pohlia*, unlike *Bryum*, will usually show some prorations on distal laminal cells.

Another feature of *Pohlia* that suggests placement in the Mniaceae is the prominent pattern of leaf buttressing which shows itself in shelf-like prominences on the stem after the leaves are removed. These prominences can be viewed in thin longitudinal sections of the stem and they are generally more than one cell in thickness. The pattern of leaf buttresses shown in *Pohlia* is also shown in such other Bryalean moss families as Mniaceae, Bartramiaceae and Aulacomniaceae, but not in Bryaceae.

- A. Stems inclined with dorsi-ventral arrangement of leaves such that dorsally inserted leaves are smaller and more narrow than ventrally inserted ones; leaves typically with some hint of a limbidium. *Epipterygium tozeri*
- A. Stems with overall erect arrangement without dorsi-ventral heterophylly; leaves typically without a limbidium. B
- B. Leaves deeply concave with the apex broadly obtuse; leafy stems pale and glossy; cells with the walls thick and pitted. *Anomobryum julaceum*
- B. Leaves various, keeled or not but never deeply concave; apices acute to acuminate or bluntly obtuse; leafy stems greenish and not glossy; cell walls not thick and pitted. C
- C. Costa filling more than 1/3 of leaf base, becoming excurrent and filling leaf apex; axillary hairs with vividly reddened basal cells. *Leptobryum pyriforme*
- C. Costa more narrow, excurrent or shorter; axillary hairs without such prominently colored basal cells. D
- D. Plant almost stemless with costa percurrent but disappearing near its base; seta erect and red-brown bearing a slightly inclined short cylindric capsule. *Discelium nudum*
- D. Plant with a stem 1 mm long or more; costa various but present to leaf base; seta and capsule various. E
- E. Plants commonly with gemmae in the axils of the upper leaves; exothelial cells short-rectangular 1.5–2.5:1; capsules short, less than 2:1. F
- E. Plants without axillary gemmae; exothelial cells isodiametric or longer than 3:1. L
- F. Gemmae 1 or at most 2 per leaf axil. G
- F. Gemmae clustered, more than 3 per leaf axil. H
- G. Leaves spreading, more or less carinate; propagula 2–4:1, with leaf primordia on their mid-regions as well as their apices. *Pohlia drummondii*
- G. Leaves erect, not carinate; propagula 1–2:1 with leaf primordia restricted to their apices. *Pohlia filum*
- H. Propagula less than 2:1 with their leaf primordia only 1–2 cells, curled over the propagulum apex, and with those propagula short-stalked. *Pohlia campotrachela*
- H. Propagula elongate, usually more than 6:1; leaf primordia erect to spreading, triangular and multicellular, sometimes absent; propagula stalked or not. I
- I. Leaf primordia on propagula triangular and foliose. J
- I. Leaf primordia absent or small geniculate to spreading peg-like structures. K
- J. Area of leaf primordia occupying only 1/3 to 1/4 of total gemma length of the elongate gemmae. *Pohlia tundrae*
- J. Area of leaf primordia occupying almost 1/2 of the length of the short oblong gemmae. *Pohlia andalusica*
- K. Propagula usually with more than 2 erect leaf primordia; plants not glossy. *Pohlia annotina*
- K. Propagula without leaf primordia or, at most, with 1–2 often geniculate structures. *Pohlia proligera*
- L. Leaf apices somewhat cucullate at least on upper portions of stem; lower leaves on stem usually black; plant of seepages in snow-melt areas of high mountains. *Pohlia obtusifolia*
- L. Leaf apices not cucullate; plant and leaves never blackened; plant of various habitats. M
- M. Vegetative leaf margins recurved at least near the base. N
- M. Vegetative leaf margins plane. P

- N. Capsules ovoid, less than 1.5:1, with little definition of a neck; plant usually with nearly spherical, multicellular rhizoidal gemmae slightly buried or surficial near base of stem. . . . *Pohlia lescuriana*
- N. Capsules pyriform to cylindrical, about 2:1; gemmae unknown in California. O
- O. Plant glaucous, tufted on seepages over schistose rocks, mostly on road cuts; peristome with exostome absent and endostome papillose. see *Mielichhoferia*
- O. Plant green to yellow green; growing on moist soil in alpine areas; exostome and endostome present but without endostome cilia. *Pohlia cardotii*
- P. Plants parvicous (look for perigonia in axils of leaves immediately below perichaetia). Q
- P. Plants dioicous. S
- Q. Plants with a white but very glossy cast; leaves erect and overlapping, often appearing almost complanate; walls of median cells thin. *Pohlia cruda*
- Q. Plants without a whitish cast; cell walls more than 2 μm thick. R
- R. Endostome segments perforate along the keel with the perforations 2–4:1; cilia present; broadly distributed species both in substrate and elevational occurrence, often in ruderal sites. *Pohlia nutans*
- R. Endostome segments much more narrowly perforate, if at all; plant of very high alpine rock crevices. *Pohlia elongata*
- S. Leaves long-decurrent; exothelial cells almost isodiametric. T
- S. Leaves not or very little decurrent; exothelial cells longer than broad. U
- T. Plants pale, whitish-green; median cells 12–20 μm wide. *Pohlia wahlenbergii*
- T. Plants green to deep-green; leaves not or very little decurrent; median cells to 10 μm wide. *Pohlia ludwigii*
- U. Leaves serrulate to low serrate near the apices. V
- U. Leaves strongly serrate at apex. X
- V. Plants of montane and coastal bogs; exothelial cells shorter; capsules 2–3:1, mostly pendent. *Pohlia sphagnicola**
- V. Plants of alpine to sub-alpine sites; exothelial cells and capsules various. W
- W. Stems of plant green to brown; exothelial cells long-rectangular, more than 8:1; capsules mostly more than 4:1 ascending to horizontal. *Pohlia bolanderi*
- W. Stems of plant reddened; exothelial cells shorter; capsules 2–3:1, mostly pendent. *Pohlia vexans**
- X. Plant vigorous with the stems 5–25 mm high; cells of exothecium isodiametric; leaves spreading, with much enlarged perichaetial bracts. *Pohlia longibracteata*
- X. Plant smaller, stems 3–8 mm high; cells of exothecium short-rectangular with the walls strongly sinuose; leaves erect or ascending and perichaetial bracts not so strongly enlarged. *Pohlia pacifica*

Polytrichastrum* G. L. Smith, 1971. see *Pogonatum

Polytrichastrum alpinum (Hedwig) G. L. Smith

Older bryological works emphasized the gross morphology of the capsule in dividing those Polytrichaceae with abundant photosynthetic lamellae filling most of the abaxial surface of the leaf. This emphasis basically meant that plants with longitudinally ridged capsules were placed in the genus *Polytrichum*, and plants with smoothly cylindrical capsules were placed in *Pogonatum*. Subsequent work emphasizing patterns of exothelial wall ornamentation and stomatal presence or absence has shown that *Polytrichastrum alpinum* has stomatal and exothelial morphology appropriate to *Polytrichum* despite its cylindrical, unridged capsules. Most works list *Polytrichum formosum* and *P. longisetum* in *Polytrichastrum* but we have become convinced that the overall morphological pattern of these latter two species place them more effectively in *Polytrichum*.

***Polytrichum* Hedwig, 1801.**

The plants that we include in this key are robust plants whose generally stiff leaves have parallel photosynthetic lamellae that run from near the base to near the tip of the adaxial surface of the leaf. In all the plants here the photosynthetic lamellae are so numerous as to cover most of the leaf width.

Species included in this key: all Polytrichaceae

Polytrichum commune Hedwig

Polytrichum formosum Hedwig

Polytrichum juniperinum Hedwig

Polytrichum longisetum Swartz ex Bridel

Polytrichum piliferum Hedwig

Polytrichum strictum Bridel

Identification of *Polytrichum* or its relatives involves making a leaf cross-section so that the distal cell of the photosynthetic lamellae can be viewed. Alternatively or additionally the lamellae can be scraped from an individual leaf with the broad side of a razor blade. On a world-wide scale, most members of the genus *Polytrichum* (and its mostly tropical relative *Pogonatum*) have the distal cells (marginal if viewed in a lamellar scrape) of somewhat larger diameter and of different morphology from the other cells of that lamella.

- | | |
|--|--------------------------------|
| A. Leaf margins entire, erect to incurved at margin. | B |
| A. Leaf margins usually dentate or, if entire, without the strong incurving of the margin. | E |
| B. Leaves strongly cucullate at apex; plant small with leaves mostly less than 5 mm long. | |
| | <i>Polytrichum sexangulare</i> |
| B. Leaves mostly flat at apex, denticulate to dentate at least at apex. | C |
| C. Leaf with a strongly hyaline apex that is reddish only in a small portion of its base, if at all. . . | |
| | <i>Polytrichum piliferum</i> |
| C. Leaf with a reddish to concolorous apex, hyaline only at extreme tip, if at all. | D |
| D. Plants mostly more than 10 cm high, occupying bogs and very wet sites, often with <i>Sphagnum</i> ; leaves rigidly erect when dry; stems densely covered with white to pale brown rhizoids. | |
| | <i>Polytrichum strictum</i> |
| D. Plants mostly shorter, occupying mesic to rather dry soil, never in bogs; leaves ascending when dry; stems with only sparse rhizoidal cover. | <i>Polytrichum juniperinum</i> |
| E. Marginal cells of the lamellae notched in cross-sectional view, without either papillae or cuticular ridges. | <i>Polytrichum commune</i> |
| E. Marginal cells otherwise. | F |
| F. Laminar cells 15–25 μm in longest diameter; mid-leaf with lamina 6 or more cells wide; capsule inconspicuously sulcate. | <i>Polytrichum longisetum</i> |
| F. Laminar cells 10–15 μm in longest diameter; mid-leaf with lamina 1–5 cells wide; capsule strongly sulcate. | <i>Polytrichum formosum</i> |

Porotrichum (Bridel) Hampe, 1863. see *Neckera*

Porotrichum bigelovii (Sullivant) Kindberg

The genus *Porotrichum* is primarily found in tropical regions with this one species broadly distributed in western North America. Many bryologists place this species in *Porothamnium* but we find the arguments unconvincing. It is recognizable by the broadly rounded costate and complanately arranged leaves with short cells. It is differentiated from the much smaller *Bryolawtonia* because the postical (nearest the stem base) leaf margins of *Porotrichum* are strongly recurved. *Porotrichum* occupies shaded to intensely shaded recesses in soil banks and rock outcrops at low to medium elevations coastally and in the California mountains.

Pseudobraunia (Lesquereux & T. P. James) Brotherus, 1905. see *Hedwigia*

Pseudobraunia californica (Lesquereux) Brotherus

Pseudobraunia is a monotypic genus endemic to western North America. It is closely related to *Hedwigia* and often grows in close association with that genus on periodically moist rock outcrops. The main basis for separation of the two genera is the exserted sporophyte of *Pseudobraunia*. Gametophytic differences, however, are such as to make field identification easy. Like *Hedwigia*, *Pseudobraunia* is ecostate and hyaline awned with very concave leaves. *Pseudobraunia* is red-brown in color compared to the gray-green of *Hedwigia*. *Pseudobraunia* has a long and flexuose awn compared with the shorter and stiff awn of *Hedwigia*.

Pseudo-calliergon (Limpricht) Loeske, 1907. see *Calliergon*

Pseudo-callierygon turgescens (T. Jensen) Loeske*

Pseudo-calliargon is a genus of semi-aquatic mosses that have brownish or yellow brown leaves ending in a blunt to rounded apex and lacking rhizoid or even nematogon placement on those leaves.

The falcate leaves of *Pseudo-calliargon angustifolium* are unusual compared with most other leaves which have been called falcate. Truly falcate leaves arch outward from their insertion as a sickle-shaped foliar structure. Plants such as *Pseudo-calliargon angustifolium* have leaves which arch outward only in their distal one-half while the proximal half of their leaf is erect and symmetrical. Similar patterns are found in such other plants as *Hamatocaulis vernicosus* and *Hypnum subimponens*.

Pseudocrossidium* R. S. Williams, 1915. see *Barbula*, *Didymodon

Pseudocrossidium crinitum (Schultz) Zander

Pseudocrossidium obtusulum (Lindberg) H. Crum & L. E. Anderson

Our two species of *Pseudocrossidium* are very different in gross morphology. *Pseudocrossidium crinitum* has been called a *Tortula* because of the hyaline awn and rather broad leaves. It lacks the C-shaped papillae that characterize most species of *Tortula* or *Syntrichia*, and the distal portions of its leaves form an acute angle with the costa. Of greater importance is the pattern of strong recurvature of the leaf margin and the reduction of the size and density of the papillae in these near marginal areas of the leaf. The muticous *P. obtusulum* resembles *P. crinitum* in that reduction of papillar prominence near the leaf margin, and its marginal leaf curvature is revolute in that the curve completes at least a single spiral as seen in leaf cross-section.

Pseudoleskeella* Kindberg, 1897. see *Lescuraea

Pseudoleskeella serpentinis P. Wilson & Norris

Pseudoleskeella tectorum (Funck ex Bridel) Kindberg in Brotherus

Pseudoleskeella has leaves mostly smaller than 1 mm long, and these leaves have short costae which typically fork and disappear before mid-leaf. The median laminal cells are typically elliptical and less than 4:1. They have a well defined area of numerous quadrate alar cells. Unlike the majority of plants in the Leskeaceae, *Pseudoleskeella* has neither paraphyllia nor laminal cell papillosity. Our two species include *Pseudoleskeella serpentinis*, a plant endemic to serpentine areas of northern California and Oregon, and *Pseudoleskeella tectorum*, a species scattered through the state but common only in our eastern deserts, primarily restricted to calcareous rocks.

Pseudoscleropodium* (Limpricht) Fleischer, 1923. see *Brachythecium*, *Scleropodium

Pseudoscleropodium purum (Hedwig) Fleischer in Brotherus

Pseudoscleropodium, everywhere in the world, behaves as if it were an introduction. It has recently become established and abundant in lawns in western Washington State, and now it has spread all the way to northwestern California. It is one of our largest julaceous mosses, and this julaceous pattern is not duplicated in *Brachythecium*. It is easily distinguished from *Scleropodium* by the strongly porose and pitted cells of the basal juxtacostal region.

Pseudotaxiphyllum* Iwatsuki, 1987. see *Plagiothecium

Pseudotaxiphyllum elegans (Bridel) Iwatsuki

Pseudotaxiphyllum has traditionally been placed with other ecostate and complanate-leaved mosses in the genus *Plagiothecium* or its non-decurrent segregate, *Isopterygium*. Modern classifications of this group of plants emphasize the presence or absence of a hyaloderm, and the presence or form of the pseudoparaphyllia. *Pseudotaxiphyllum* is a genus without either a hyaloderm or pseudoparaphyllia. Our species is easily recognized because it almost always has clusters of microphyllous branchlets in the upper leaf axils. These are asexual reproductive devices as they become detached from the parent plant. *Pseudotaxiphyllum elegans* is abundant on soil bank and rock faces especially in dimly lighted areas in the lowland areas of coastal California.

Pterigynandrum* Hedwig, 1801. see *Lescuraea

Pterigynandrum filiforme Hedwig

Pterigynandrum filiforme is one of the smallest julaceous mosses. It has ecostate, concave leaves with abundant foliose paraphyllia and strongly prorate laminal cells. It is abundant on the bark of coniferous trees in montane forests throughout the state. It is not uncommon on the face of rock outcrops in the same forests.

Pterogonium* Swartz, 1801. see *Antitrichia

Pterogonium gracile (Hedwig) J. E. Smith

Pterogonium gracile, the only world-wide species of the genus, shares with *Antitrichia* a large suite of characters. Among the most noteworthy of these features are 1) costate leaves with the costa flattened basally; 2) coronate-papillose terminal cells of many of the leaves; 3) tapering and determinate lateral branching; 4) strongly julaceous main stems and branches; 5) long acicular perichaetia; 6) elongate-cylindrical, exserted capsules. The only distinguishing feature between the genera is the presence of prorate-papillosity on the median cells of *Pterogonium*. *Pterogonium* is most easily confused in the field with *Antitrichia californica*, a plant with similar julaceous and tapering axes. A quick hand-lens assessment will, however, show the recurved leaf apices and narrowly but regularly recurved margins of the *Antitrichia*. When dry, the plants of *Pterogonium* have a pattern of curling of the tapered lateral branches that, uniquely among mosses, may resemble the profile of a many-toed bird's foot.

***Pterygoneurum* Juratzka, 1882.**

Mosses included in this section are costate acrocarps with hyaline awns. Inserted on the adaxial face of the costa are 2–4 rather high photosynthetic lamellae, and these will be obvious as lamellae even under the dissection microscope. *Pterygoneurum* can be confused only with the two other Pottiaceae with photosynthetic processes on the adaxial face of the leaf. The lamellae on the leaves of *Pterygoneurum* are not crowded, and are therefore easily seen as separate entities. In contrast *Aloina* and *Crossidium* (with the exception of *C. aberrans*) have such crowded photosynthetic filaments that dissection microscopes may not easily allow visual resolution of the individual filaments.

Species included in this key: all Pottiaceae

- Pterygoneurum californicum* H. Crum
- Pterygoneurum lamellatum* (Lindberg) Juratzka
- Pterygoneurum ovatum* (Hedwig) Dixon
- Pterygoneurum sessile* (Bridel) Juratzka

This is the most widespread in California of the three Pottiaceous genera with adaxial photosynthetic processes. Whereas *Crossidium* and *Aloina* are largely plants of calcareous sites, our four species of *Pterygoneurum* largely seem indifferent to the presence of calcium ions. *Pterygoneurum* is not only a plant of soil but our two common species are regular occupants of the tops of decomposing grass tussocks in desert habitats. Of the four species of the genus in California, only *P. ovatum* and *P. sessile* are of regular occurrence; the other two species are very local and rare.

- A. Leaves on at least some specimens elongate, somewhat spatulate, 3–4:1; peristome present, fugacious and clinging to operculum; urn oblong to cylindric, 4–6:1; cells papillose on back, at least in the distal end of the leaves. *Pterygoneurum lamellatum*
- A. Leaves ovate, often broadly so, never spatulate; peristome absent; urn mostly ovoid to hemispheric; cells smooth or somewhat papillose dorsally near leaf apex. B
- B. Sporophyte emergent or exserted with seta longer than the urn. *Pterygoneurum ovatum*
- B. Sporophyte immersed on a seta shorter than the urn. C
- C. Spores densely papillose; calyptra mitrate; median laminal cells mostly with corner thickenings. *Pterygoneurum sessile*
- C. Spores smooth; calyptra cucullate; median laminal cells evenly thick-walled. *Pterygoneurum californicum*

Ptilium* De Notaris, 1867. see *Hylocomium*, *Hypnum

Ptilium crista-castrensis (Hedwig) De Notaris*

Ptilium is a monotypic genus widespread throughout moist forests in all northern North America and Eurasia. It has not yet been found in California. It is a genus segregated from *Hypnum* on the basis of its strongly plicate and decurrent leaves, and on the basis of a regularly pinnate and plumose branching pattern with the branches parallel and contiguous; branches strongly hamate at apices.

***Ptychomitrium* Furnrohr, 1829.**

The mosses keyed in this section are costate acrocarps with strongly crispate leaves. We have in California only one described species, and this has strongly dentate leaves. Its sporophytes are typically polysetous (with more than one sporophyte emerging from a perichaetium). The calyptra of *Ptychomitrium*

is distinctive: strongly plicate and basally fringed, campanulate and sheathing most of the capsule. Our species is almost always petricolous on both acid and alkaline rocks.

Species included in this key: all Ptychomitriaceae

Ptychomitrium gardneri Lesquereux

Ptychomitrium serratum (C. Müller Hal.) Bruch & W. P. Schimper *ex* Bescherelle*

Ptychomitrium sinense (Mitten) A. Jaeger*

The genus *Ptychomitrium* is not easily confused with any other local moss. It usually has sporophytes, and the polysetous condition will usually be obvious. Species determination of a *Ptychomitrium* requires inspection of the larger and more distally placed leaves on a stem. The dentate margin of more proximally placed leaves is often reduced relative to the more distal leaves. Leaf cross-sections are important in species distinction, and these too are best obtained from larger leaves on distal portions of the stems. Cross-sections should be made from areas of the leaf immediately above the shoulders.

An additional genus in the family Ptychomitriaceae may eventually be found in the state. *Campylostelium*, a moss of higher elevations in such more northern areas as Washington State, has the basally fringed calyptra of *Ptychomitrium* but that calyptra is not plicate and it covers only the strongly rostrate operculum. It is much smaller than our species of *Ptychomitrium*, and its capsule is placed on a cygneous seta.

The shape and size of the marginal teeth are specially important in *Ptychomitrium*. Our species differ in number of cells within each tooth; in being sharply pointed or blunt; and in having the teeth upwardly oriented to incurved versus outwardly spreading.

- A. Leaf margins entire, plane to erect; leaves ovate-lanceolate without significant differentiation of a narrowed acumen. *Ptychomitrium sinense**
- A. Leaf margins dentate, recurved at least near base; leaves lanceolate but contracted below the middle into a well-defined acumen. B
- B. Marginal teeth of distal ¼ of leaf sharply pointed and diverging from margin at more than a 30 degree angle; mid-leaf cross-section unistratose except for a narrowly bistratose margin; leaf with a well demarcated acumen that includes about ½ or more of that leaf. . . . *Ptychomitrium gardneri*
- B. Marginal teeth of leaf mostly rather blunt or pointed but inflexed relative to margin; mid-leaf cross-section various; acumen markedly shorter. C
- C. Leaf mostly bistratose above the middle; basal cells rectangular but with lateral walls not sinuose; marginal teeth variable with some of them somewhat sharply pointed and inflexed in plane of leaf. *Ptychomitrium* species A
- C. Leaf mostly unistratose; rectangular basal cells with lateral walls sinuose; marginal teeth uniformly blunt. *Ptychomitrium serratum**

Pyramidula* Bridel, 1818 [1819]. see *Funaria

Pyramidula tetragona (Bridel) Bridel

Pyramidula is a typical member of the Funariaceae: an acrocarpous moss growing on disturbed or arid habitats with the typical costate leaves and thin-walled cells with a basically rectangular rather than hexagonal outline, thus different from the Bryaceae. The distinguishing feature of *Pyramidula* is the 4-ribbed calyptra with a basically square outline of its lower portion when viewed in cross-section. *Pyramidula*, recently documented for California, should be sought in coastal southern California.

***Racomitrium* Bridel, 1819 [1818].**

Racomitrium is an extensively branched plant that, nevertheless, has perichaetia on the ends of erect axes and is therefore technically acrocarpous (or cladocarpous). The genus is costate and usually with hyaline awns. The diagnostic feature for the genus is in the lateral walls of its laminal cells. All members of the Grimmiaceae have sinuose lateral walls but those walls of *Racomitrium* are so much more sinuose as to provide a means of automatically recognizing the genus.

Species included in this key: all Grimmiaceae

Grimmia leibergii Paris

Grimmia ramondii (Lamarck & A. P. de Candolle) Margadant

Racomitrium aciculare (Hedwig) Bridel

Racomitrium affine (Schleicher *ex* Weber & D. Mohr) Lindberg

Racomitrium brevipes Kindberg *in* Macoun*

Racomitrium depressum Lesquereux

Racomitrium elongatum Ehrhart ex Frisvoll
Racomitrium ericoides (Hedwig) Bridel
Racomitrium fasciculare (Hedwig) Bridel
Racomitrium heterostichum (Hedwig) Bridel
Racomitrium lanuginosum (Hedwig) Bridel
Racomitrium lawtonae Ireland
Racomitrium macounii Kindberg
Racomitrium microcarpon (Hedwig) Bridel
Racomitrium molle Cardot
Racomitrium norrisii Bednarek-Ochyra & Ochyra
Racomitrium obesum Frisvoll
Racomitrium occidentale (Renauld & Cardot) Renauld & Cardot
Racomitrium pacificum Ireland & Spence
Racomitrium pygmaeum Frisvoll*
Racomitrium rysardii Bednarek-Ochyra*
Racomitrium sudeticum (Funck) Bruch & W. P. Schimper
Racomitrium varium (Mitten) A. Jaeger

Work with *Racomitrium* requires leaf cross-sections from approximately the middle of the leaf (excluding the awn). The cross-section should show the number of cell layers in the costa, the pattern of uni- and bi-stratose areas of the lamina, and it should show any flattening or grooving of the abaxial surface of the costa. We are most appreciative of the detailed studies conducted on this genus by Dr. Halina Bednarek-Ochyra. Her interpretations have been completely followed in this work. Those species of *Racomitrium* which are described as papillose have been described by other authors as “pseudopapillose.” The papillae of *Racomitrium* are patterns of bumps on the surface of the transverse and lateral walls of the leaf cells, and these papillae do not appear over the lumina.

Among the more difficult to understand characters in *Racomitrium* is the difference between sinuosity and porosity of the lateral cell walls (see *R. microcarpum*). “Sinuosity” is basically a character of the Grimmiaceae and of few other mosses. The lateral wall is itself sinuose and thus retains a constant thickness on each side. Where one side of the wall curves outward, that portion of the laterally adjacent wall curves inward. “Porosity” is a character of many mosses. It is a feature of thick-walled cells with basically straight lateral walls. The irregularities of those lateral walls are formed from localized thin portions in which the walls of laterally adjacent cells have thin places coinciding on each side of the wall. While the majority of *Racomitrium* in California are petricolous, some species also occur on soil and humus, especially in the northwest portion of the state. The genus also displays a wide suite of microhabitats ranging from dry walls to seasonally or regularly submerged rocks in streams and rivers.

- A. Leaves with abaxial ridges on costa, never with a hyaline awn. *Grimmia ramondii*
- A. Costa not ornamented on abaxial surface. B
- B. Leaves strictly muticous. C
- B. At least some of the leaves in a clone with an hyaline awn. M
- C. Leaf cells with low papillae over lumen or over lateral walls. D
- C. Leaf cells smooth. I
- D. Leaves oblong, with a broad, rounded, often dentate to serrulate apex; plant aquatic or in high elevation seepages. E
- D. Leaves lanceolate with the apex acuminate to rounded but always with the apex entire and considerably narrowed from below the leaf middle. G
- E. Margins at mid-leaf bistratose to 10 cells wide; papillosity at mid-leaf very low and inconspicuous; leaf apices primarily acute. *Racomitrium norrisii*
- E. Leaf unistratose throughout; papillosity at mid-leaf conspicuous even at lower magnifications; leaf apices primarily obtuse. F
- F. Costa ending near mid-leaf, only 2–3 cells wide distally; leaves elliptical to oblong-elliptical, broadly rounded and nearly entire at apex. *Racomitrium molle*
- F. Costa extending nearly to leaf apex, more than 4 cells wide distally; leaves broadly lingulate to oblong-lanceolate, rounded obtuse or even with a slight acumination, usually erose-dentate at apex. *Racomitrium aciculare*
- G. Alar cells much inflated; apex on at least some leaves with a hyaline awn; operculum 0.6–0.9 as long as urn. *Racomitrium varium*
- G. Alar cells not inflated; apex consistently muticous; operculum relatively shorter. H
- H. Median leaf cells elongate, more than 3:1; stems with numerous short, lateral branches. *Racomitrium fasciculare*

- H. Median leaf cells mostly isodiametric; stems without a close grouping of short lateral branches. *Racomitrium ryszardii**
- I. Leaves somewhat laterally twisted when dry; margin bistratose in 2–4 rows at least from near the apex to below the middle; plants with a red brown cast. *Racomitrium macounii*
- I. Leaves appressed to falcate when dry; margin unistratose throughout or with rather more limited bistratose streaks; plants mostly without such a red brown cast. J
- J. Leaf apices bluntly rounded, often crenulate; margin unistratose, usually somewhat crenulate distally, inconspicuously recurved, often plane on one side. K
- J. Leaf apices acute to bluntly acute, not at all crenulate; margin often in part bistratose, mostly with a rather long area of recurvature on both sides especially near the leaf middle. L
- K. Leaves concave, mostly longer than 3 mm; alar cells mostly thin-walled, sometimes decurrent, in a poorly demarcated region; plants growing in streams, mostly in high mountains. *Racomitrium depressum*
- K. Leaves smaller and not concave; alar cells short and thick-walled, often porose, in a well demarcated, often auriculate group; plants growing on wet rocks in lowlands. ... *Racomitrium pacificum*
- L. Costa mostly less than 80 μ m broad near base, near abaxial apex so convex as to appear almost cylindrical; leaf apex rather gradually acuminate; inner perichaetial leaves only slightly differentiated from adjacent vegetative leaves. *Racomitrium sudeticum*
- L. Costa mostly broader, near apex not so abaxially convex; leaf apex acute; inner perichaetial leaves very much reduced in size, hyaline or nearly so. *Racomitrium affine*
- M. Hyaline awn prominently papillose. N
- M. Hyaline awn smooth or absent (note that the awn may sometimes be toothed and appear papillose). Q
- N. Cells of lamina smooth, with a lumen:wall ratio less than 1:1; hyaline awn decurrent a distance almost equal to the length of the rest of the awn. *Racomitrium lanuginosum*
- N. Cells of lamina papillose; walls thinner; awn decurrency short or absent. O
- O. Costa ending at about $\frac{1}{2}$ – $\frac{3}{4}$, frequently forked distally; leaves mostly less than 3:1, not keeled except at extreme apex. *Racomitrium ericoides*
- O. Costa extending to the base of the acumen or beyond, not forked distally; leaves mostly more than 4:1, strongly keeled in distal $\frac{1}{3}$ P
- P. Leaves with distinct and somewhat inflated alar cells; costa obscured by its position in the deep central keel; abundant plant on most substrata and at most altitudes. *Racomitrium elongatum*
- P. Leaves with alar cells not so inflated; costa not so obscured; plant rarely present at higher elevations in Washington State. *Racomitrium pygmaeum**
- Q. Costa strongly convex abaxially, distally grooved or ridged; awn terete, strongly spinulose, not flexuose; plant green and sparsely branched. *Racomitrium occidentale*
- Q. Costa not distally grooved or ridged. R
- R. Median leaf cells with small to rather large papillae over the lateral walls. S
- R. Median leaf cells smooth in lateral or cross-sectional view. T
- S. Plant mostly gray- to glaucous green; alar cells much inflated; costa at mid leaf lying in a poorly defined channel, less than 8 cells wide; operculum 0.6–0.9 times as long as urn. *Racomitrium varium*
- S. Plants olive-green to fuscous or blackish; alar cells poorly differentiated; costa at mid-leaf in a well-defined channel, about 8 cells wide; operculum less than 0.5 times the length of the urn. *Racomitrium brevipes**
- T. Leaf margins at mid-leaf bistratose in a band two or more cells wide; costa dorsally convex and mostly 4-stratose; plants brown to russet. *Racomitrium macounii*
- T. Leaf margins at mid-leaf unistratose or with the bistratosity only one cell wide; costa mostly not so thick; plants green to blackish green. U
- U. Basal cells of leaf thick-walled and porose but without sinuosities; basal marginal cells forming a distinct limbidium of several cell rows; costa near base only 3–4 cells wide. *Racomitrium microcarpon*
- U. Basal cells of leaf not differentiated, not forming a limbidium; costa near base 5–9 cells wide. ... V
- V. Basal marginal cells quadrate to rectangular with transverse walls markedly thicker than lateral walls; costa near base flattened and somewhat grooved, usually with a small and thin abaxial stereid band. *Grimmia leibergii*
- V. Basal marginal cells mostly rectangular without transverse wall thickening; costa near the base not strongly flattened or grooved; mostly without stereids. W
- W. Margin recurved from near the base to near the awn; awn of dry leaf mostly not squarrose. ... X

- W. Margin mostly not recurved above the middle; awn of dry leaf usually at least somewhat squarrose. Z
- X. Leaf margin at mid-leaf mostly bistratose; leaf lamina somewhat contracted at intersection with the terete and rigid awn. *Racomitrium obesum*
- X. Leaf margin at mid-leaf mostly unistratose; leaf lamina not at all contracted; awn rather broad and flat at base. Y
- Y. Costa adaxially grooved to canaliculate immediately below mid-leaf; costa cross-section mostly only 2 cells thick at mid-leaf. *Racomitrium heterostichum*
- Y. Costa not at all adaxially grooved, or perhaps slightly so near leaf apex; costa cross-section mostly 3 cells thick at mid-leaf. *Racomitrium affine*
- Z. Awn mostly about 1 mm long, decurrent; leaves to 3 mm long; marginal cells in alar region rectangular and not much differentiated from the interior cells. *Racomitrium lawtonae*
- Z. Awn mostly shorter, not decurrent; plant smaller; marginal cells in alar region hyaline in 1–2 marginal rows; urn of capsule mostly shorter than 2 mm. *Racomitrium sudeticum*

***Rhizomnium* (Mitten *ex* Brotherus) T. Koponen, 1968.**

Mosses included in this section are broad-leaved acrocarps with rounded leaf apices. Cells are isodiametric or short-hexagonal, and there is a strong limbidium of elongate and thick-walled cells. The leaf margin is absolutely entire to the apex.

Species included in this key: all Mniaceae

- Mnium blyttii* Bruch & W. P. Schimper
- Rhizomnium glabrescens* (Kindberg) T. Koponen
- Rhizomnium gracile* T. Koponen*
- Rhizomnium magnifolium* (Horikawa) T. Koponen
- Rhizomnium nudum* (E. Britton & R. S. Williams) T. Koponen*
- Rhizomnium pseudopunctatum* (Bruch & W. P. Schimper) T. Koponen
- Rhizomnium punctatum* (Hedwig) T. Koponen

Mosses have several types of rhizoid origin. Often rhizoids originate from cells at the ab- or adaxial leaf insertion. Sometimes rhizoids originate from cells of the leaf, most often the abaxial face of the costa or lamina. In the Bryales and some other groups there are special types of rhizoids based upon patterns of origination on the stem. Macronemata form a halo around a bud primordium, and these are seemingly homologous to the pseudoparaphyllia of many pleurocarpous mosses. Micronemata come from cells scattered, or arranged in longitudinal rows, on the stem surface. Even when the rhizoids are absent, the cells from which micronemata arise will show as somewhat enlarged cells without chloroplasts. It should be noted here that there is no necessary size correlation between the so-called “macronemata” and the “micronemata.”

One of the major taxonomic subdivisions of the genus *Mnium* concerns the presence or absence of micronemata. In general, a plant with micronemata has a dense coating of rhizoids over the entire stem up to the bases of the youngest leaves. In general, a plant without micronemata has dense rhizoids restricted to clusters arising from some of the more proximal portions of the stem.

- A. Micronemata present (Note: younger or poorly developed stems may lack the micronemata but the initials will still be present and visible in a stem whole-mount). B
- A. Micronemata and their initials consistently absent. D
- B. Leaves and plant small with leaves seldom exceeding 4 mm long; costa short, ending at about ¾; leaf border unistratose. *Rhizomnium gracile**
- B. Leaves and plant larger; costa percurrent or ending within a few cells of apex; leaf border one or more cells thick. C
- C. Costa confluent with the limbidium or ending within 2–3 cells of the limbidium; plant dioicous; leaves on at least the well developed stems more than 7 mm long. *Rhizomnium magnifolium*
- C. Costa ending several cells below the limbidium; plant synoicous; leaves smaller. *Rhizomnium pseudopunctatum*
- D. Limbidium obvious and extending to the apex; costa mostly confluent with the limbidium and apiculate. E
- D. Limbidium narrow near base and seldom extending to apex; costa of most leaves subpercurrent with apex hardly apiculate. F
- E. Laminal cells mostly about 2:1 with walls evenly thickened; stems reddish. *Rhizomnium punctatum*

- E. Laminal cells mostly shorter with end walls having small corner thickenings; stems brownish. *Rhizomnium glabrescens*
- F. Leaves nearly orbicular; limbidium mostly not reaching leaf apex or sometimes one cell wide; plant green after death; leaves not decurrent. *Rhizomnium nudum**
- F. Leaves obovate, mostly more than 1.5:1; limbidium several cells wide at apex with costa percurrent or nearly so; plant with post-mortal reddish blush; leaves decurrent by means of a 1-2 cell wide strip that reaches nearly to base of next lower leaf. *Mnium blyttii*

Rhytidiadelphus* (Limpricht) Warnstorf, 1906. see *Hylocomium

Rhytidiadelphus loreus (Hedwig) Warnstorf

Rhytidiadelphus squarrosus (Hedwig) Warnstorf

Rhytidiadelphus subpinnatus (Lindberg) T. Koponen*

Rhytidiadelphus triquetrus (Hedwig) Warnstorf

In California, *Rhytidiadelphus* is one of our more important "feather mosses," so named because of the plumose branching from a somewhat elevated, decumbent or erect, central stem axis. Most of these feather mosses are quite large, and they usually form extensive, nearly pure colonies on soil or on thin soil over rock outcrops. *Rhytidiadelphus* stands out among the feather mosses as a plant without paraphyllia, and with a strong double costa which ends near mid-leaf. *Rhytidiadelphus* in California is infrequently encountered and restricted to the northwest part of the state. *Rhytidiadelphus squarrosus* is, however, beginning to spread as a lawn weed in that area.

Rhytidiopsis* Brotherus, 1908. see *Hylocomium

Rhytidiopsis robusta (W. J. Hooker) Brotherus

Rhytidiopsis is a monotypic genus endemic to western United States but so far found only once in California. It grows on leaf litter in coniferous forests where it seems adapted to the compacting effects of a heavy winter snow cover. It appears in the field as a *Rhytidiadelphus* but the dense coating of paraphyllia on its stems and branches is obvious even with a hand-lens.

Rhytidium* (Sullivant in A. Gray) Kindberg, 1882. see *Hylocomium

Rhytidium rugosum (Hedwig) Kindberg*

Rhytidium is a monotypic genus not yet found in California. It has a strangely discontinuous range throughout the world with the nearest locality being northwest Oregon. It is immediately recognizable in the field as a large pinnate moss mostly growing in erect plumes. Unlike other feather mosses (*Rhytidiadelphus*, *Hylocomium*) it has a strong single costa and the leaf laminae are obviously undulate whether wet or dry.

Roellia* Kindberg, 1897. see *Bryum

Roellia roellii (Brotherus ex Röhl) Andrews in H. Crum

Roellia is a monotypic genus that appears as a very large *Bryum* but its cells are among the largest of our local bryophytes. When one encounters a large and comose acrocarpous moss on forest litter, a quick look for the large cells will establish its identity. Many earlier works considered *Roellia roellii* merely to be a large *Bryum* (*Bryum sandbergii*). Now, *Roellia* is transferred not only out of *Bryum*, but also out of the Bryaceae into the Mniaceae, a decision with which we agree.

Sanionia* Loeske, 1907. see *Drepanocladus

Sanionia uncinata (Hedwig) Loeske

The genus *Sanionia* was included in *Drepanocladus* by most of the early workers in bryology. It is easily recognized because of the circinate (so falcate as to describe more than 180° of arc) and strongly plicate, costate leaves. Most keys emphasize the presence of a well differentiated hyaloderm but that feature can be seen even without a stem cross-section. Normal patterns of leaf removal on a stem of *Sanionia* will show leaves that seem to have enlarged and thin-walled rectangular cells across the entire base. These cells are not cells of the leaf proper but they are cells of the enlarged outer cortex (the hyaloderm) of the stem. This technique of viewing the hyaloderm is also effective in *Hygrohypnum ochraceum* but the hyaloderm of some of the hyalodermous Hypnaceae does not so easily peel from the stem.

Sarmentypnum* Tuomikoski & T. Koponen, 1979. see *Calliergon

Sarmentypnum sarmentosum (Wahlenberg) Tuomikoski & T. Koponen*

Sarmentypnum is one of a group of aquatic pleurocarps with reddish pigmentation, blunt leaves and nematogons in distal portions of the leaf lamina. Among these mosses it stands out for its elliptical leaves with those leaves pressed into a blunt bud. *Sarmentypnum sarmentosum* has been placed by Hedenäs in the genus *Warnstorfia* but we are uncomfortable with that placement. *Sarmentypnum* is not yet known from California but we expect it in some of the calcareous fens of the Marble Mountain area of northern California.

***Schistidium* Bruch & W. P. Schimper in Bruch & W. P. Schimper, 1845.**

Mosses treated in this section are blackish acrocarps usually with a reddish blush. The lanceolate to ovate-lanceolate leaves may or may not have a hyaline awn. Most species have a rather large number of quadrate cells in the alar region, and they often lack the transverse wall thickening of the basal marginal cells—a feature of many species of the closely related *Grimmia*. The definitive feature is the immersed and systylious capsules—the latter feature is never present in *Grimmia*.

Species included in this key: all Grimmiaceae

- Schistidium agassizii* Sullivant & Lesquereux in Sullivant
- Schistidium atrichum* (C. Müller Hal. & Kindberg) W. A. Weber
- Schistidium cinclidodonteum* (C. Müller Hal. in Röhl) Bremer
- Schistidium confertum* (Funck) Bruch & W. P. Schimper
- Schistidium dupretii* (Thériot) W. A. Weber
- Schistidium flaccidum* (De Notaris) Ochyra
- Schistidium maritimum* (Turner ex Scott) Bruch & W. P. Schimper
- Schistidium occidentale* (E. Lawton) Churchill in Funk & D. R. Brooks
- Schistidium platyphyllum* (Mitten) Persson in Persson & Gjaerev
- Schistidium rivulare* (Bridel) Podpera
- Schistidium strictum* (Turner) Loeske*
- Schistidium tenerum* (J. E. Zetterstedt) E. Nyholm

Schistidium has frequently been considered to be merely an infrageneric category within *Grimmia*. We have discussed distinction of the two genera in the section on *Grimmia*. Species of *Schistidium* tend to occupy different ecological sites from those of *Grimmia*. *Schistidium* is most common on rock outcrops in areas of occasional submergence. It is especially common in sheet drainage areas over rock outcrops. Most species of *Schistidium* can be found with capsules if one looks carefully in the field. The glossy red urns of the sporophytes of most *Schistidium* are quite obvious when one looks at moist plants. Species that sparingly produce sporophytes will often have those sporophytes on plants on the downhill edge of the clone. Sterile material thought to be *Schistidium* might profitably be keyed both in the *Schistidium* and in the *Grimmia* keys.

Recent work by Hans Blom has been invaluable in our understanding of *Schistidium*. Monographic study of California *Schistidium* would be a worthwhile enterprise.

- A. Leaves muticous. B
- A. At least the perichaetial leaves with hyaline awns; median laminal cells extending along the margin nearly to the leaf base. I
- B. Leaves at least in the lower portion of the stem typically more than 4:1. C
- B. Leaves typically broader. F
- C. Plants occasionally washed by salt spray of the ocean; not adaxially grooved or with sinuose rectangular cells on adaxial surface; costa cross-section exhibiting a strong abaxial stereid band. *Schistidium maritimum*
- C. Plants found away from immediate maritime rocks; costa cross-section without stereid bands. . . D
- D. Leaves almost consistently bi- to tri-stratose above the middle; costa flattened at the base and merging imperceptibly into the bistratose juxtacostal basal lamina. . . *Schistidium cinclidodonteum*
- D. Leaves mostly unistratose throughout or sometimes bistratose at extreme apex; costa at base terete and well set-off from adjacent lamina. E
- E. Margin typically multistratose to mid-leaf; median leaf cells typically less than 10 µm long; capsule ovoid to short cylindric, not wide-mouthed. *Schistidium occidentale*
- E. Margin, except near leaf apex, mostly unistratose or sparingly bistratose; median leaf cells typically more than 10 µm long; capsule flaring at mouth when dry. *Schistidium agassizii*
- F. Upper leaf margin typically denticulate; plant usually submerged on riverside rocks. *Schistidium rivulare*

- F. Upper leaf margin entire; plant seldom submerged. G
G. Leaves less than 1 mm long, not recurved or only minutely so at the base; cells 4–8 μm broad. *Schistidium atrichum*
G. Leaves on well developed stems mostly over 1 mm long; margins recurved to near the middle; cells 7–10 μm broad. H
H. Urn ovoid, not much broadened to the apex; leaves to 1.5 mm long. *Schistidium dupretii*
H. Urn broad at the mouth, gradually narrowed to the base; leaves mostly more than 2 mm long. *Schistidium platyphyllum*
I. Leaf margins plane to incurved; leaves mostly long-lanceolate, more than 6:1; awn very minute, mostly less than 5 cells in length, smooth. *Schistidium cinclidodonteum*
I. Leaf margins recurved, at least on one side near base. J
J. Leafy stems less than 0.5 mm wide and mostly less than 25 mm long; leaves less than 1 mm long; plants forming wiry chestnut-brown turfs on seepages at high elevations. *Schistidium tenerum*
J. Plants and leaves larger. K
K. Leaves with at least a few papillae on dorsal surface, often rather densely covered; urn broadened toward the mouth; peristome spreading from mouth of urn. *Schistidium strictum**
K. Leaves smooth throughout; urn evenly ovoid; peristome erect or absent. L
L. Peristome absent or present as irregularly truncate segments. *Schistidium flaccidum*
L. Peristome present and well developed. M
M. Vegetative leaves mostly more than 1.5 mm long with the perichaetial leaves exceeding 3 mm long; peristome teeth deep red, not or very little cribose; transverse walls of basal marginal cells not thickened. *Schistidium* species A
M. Vegetative leaves and perichaetial leaves smaller; peristome teeth pale- or bleached red-brown, strongly cribose; transverse walls of basal marginal cells markedly thicker than the lateral walls. N
N. Leaves frequently with a hyaline awn and with that awn terete and serrate on its entire circumference; plant when moist with leaves spreading, often almost squarrose. *Schistidium* species B
N. Hyaline awn mostly found on some of the perichaetial leaves, only occasionally on vegetative leaves; plant when moist with leaves ascending to erect-ascending. *Schistidium confertum*

Schistostega* D. Mohr, 1803. see *Fissidens

Schistostega pennata (Hedwig) Weber & D. Mohr*

Schistostega occupies humid forests in Oregon and northward. It is unique among Northern Hemisphere mosses in having a protonema that appears to fluoresce in the intensely shaded recesses to which it is restricted. Close examination for such fluorescence in recesses in trail banks or under root wads may reveal its presence in northern California. *Schistostega* is one of our strictly distichous mosses but it differs from the others in that the basal (postical) margin of each leaf fuses with the antical margin of the next leaf below to produce a leafy stem similar to the compound leaf of the fern, *Osmunda*.

Schizymenium* Harvey in W. J. Hooker, 1840. see *Pohlia

Schizymenium shevockii A. J. Shaw

The largely tropical and Southern Hemisphere genus *Schizymenium* closely resembles *Mielichhoferia*. Both genera have a similar and distinctive blue-green to glaucous appearance, especially in distant view. *Schizymenium* has recently been found in southern California on metamorphic rocks like those occupied by *Mielichhoferia*. The two genera can be distinguished by cryptic differences of the peristome and, compared with *Mielichhoferia* spp., our species of *Schizymenium* has larger median cells and more acute, plane-margined leaves.

***Scleropodium* Bruch & W. P. Schimper, 1853.**

The mosses included in this section are costate pleurocarps with smooth leaves and julaceous stems and branches. Typically, there is some differentiation of an alar region either of numerous rectangular or quadrate cells. At least the upper leaf margins have some serrulation or serration.

Species included in this key: all Brachytheciaceae

- Cirriphyllum cirrosum* (Schwägrichen in Schultes) Grout*
Pseudoscleropodium purum (Hedwig) Fleischer in Brotherus
Scleropodium californicum (Lesquereux) Kindberg
Scleropodium cespitans (C. Müller Hal.) L. Koch

- Scleropodium colpophyllum* (Sullivant) Grout
- Scleropodium julaceum* E. Lawton
- Scleropodium obtusifolium* (Mitten) Kindberg in Macoun
- Scleropodium touretii* (Bridel) L. Koch

The genus *Scleropodium* reaches its greatest world diversity in California. Here, it grows on a variety of habitats ranging from seasonally dry woodlands, very moist forests, and even grasslands. Various *Scleropodium* species can be found on soil, rock, tree bases, and even submerged in rapidly flowing streams. It is easily recognized as Brachytheciaceae by the pleurocarpous and prostrate habit with the costate leaves having that costa ending in a short spine. The diagnostic character of the genus within the Brachytheciaceae is the julaceous habit—a feature possessed even by the somewhat complanate *Scleropodium colpophyllum*. A cryptic character of uniform application throughout the genus is the pattern of the enlarged laminal cells of the leaf base covering the adaxial surface of the costa base. Note, however, that this unusual feature may be shown by some species of *Brachythecium*.

- A. Interior basal cells of leaf strongly porose; leaves decurrent; plants large with leaves mostly more than 2 cm long; leaf apices narrowed to a long acumen or short apiculus. B
- A. Interior basal cells of leaf not porose; rather thin-walled and somewhat inflated if plant is large; leaf apices various. C
- B. Leaves with an abrupt short and reflexed acumen; plant restricted to lawns and similar disturbed areas. *Pseudoscleropodium purum*
- B. Leaves with a very narrow long acumen which is at least ¼ the length of the deeply concave main portion of that leaf; plant of wet and forested areas. *Cirriphyllum cirrosu**
- C. Leaves 0.6–1.4 mm wide; cells across the leaf base rectangular (6–10:1) in one or two series. D
- C. Leaves 0.3–0.8 mm wide; cells across the leaf base quadrate to short-rectangular (1–3:1) in up to six series. G
- D. Branches variable with some leaves spreading to erect-spreading and only faintly concave while other branches are strongly julaceous. *Scleropodium colpophyllum*
- D. Branches on the entire plant similar and strongly julaceous. E
- E. Leaves on at least some stems with a short-acuminate, recurved apiculus; plant not aquatic but normally on moist soil. *Scleropodium touretii*
- E. Leaves never with a recurved apiculus; plant typically aquatic and usually in flowing water. . . . F
- F. Leaves orbicular or nearly so; plant with even the ultimate branchlets rigidly spreading. *Scleropodium* species A
- F. Leaves about 1.5 times as long as broad; plant flaccid, especially the ultimate branchlets. *Scleropodium obtusifolium*
- G. Leaves broadest near the base and gradually tapering to the acute apex; stems not very julaceous but growing in thin, straggling mats; seta papillose throughout; capsule curved and asymmetric. *Scleropodium californicum*
- G. Leaves broadest at about ½ and more or less abruptly contracted to the somewhat obtuse apex; stems, seta and capsule various. H
- H. Branches strongly julaceous; capsule curved and asymmetric. *Scleropodium julaceum*
- H. Branches usually weakly julaceous; capsule erect to inclined. *Scleropodium cespitans*

Scopelophila* (Mitten) Lindberg, 1872. see *Scouleria

Scopelophila cataractae (Mitten) Brotherus

Scopelophila cataractae is one of the mosses often called “copper mosses” because of the apparent restriction to copper-containing rocks. It is interesting that the only known occurrence of the species in California is near the town of Copperopolis, an area of past copper-mining activities. In California, *Scopelophila* shares this ecological habit with the completely unrelated *Mielichhoferia elongata* and *Schizymenium shevockii* (Mielichhoferiaceae). Both *Scopelophila* and *Crumia* occupy perennial seepages, and they have a similar pattern of a limbidium of thick-walled and enlarged cells. Unlike *Crumia*, however, *Scopelophila* has smooth, not papillose median laminal cells.

***Scouleria* W. J. Hooker, 1829 [1830].**

The mosses treated in this section are aquatic or semi-aquatic plants with large and broad leaves, obtuse or rounded at the apex. The marginal cells of the leaves are quadrate like the median laminal cells but those marginal cells are larger and thick-walled forming an opaque border easily seen under the dissection microscope.

Species included in this key: all Scouleriaceae except *Crumia* and *Scopelophila* (Pottiaceae) and *Schistidium* (Grimmiaceae)

- Crumia latifolia* (Kindberg ex Macoun) W. B. Schofield
- Schistidium rivulare* (Bridel) Podpěra
- Scopelophila cataractae* (Mitten) Brotherus
- Scouleria aquatica* W. J. Hooker in Drummond
- Scouleria marginata* E. Britton

Scouleria is one of a large number of mosses growing in rapidly flowing, unpolluted rivers and streams. Perhaps as a survival strategy these seasonally submerged mosses have evolved a differentiated, thick-walled margin that seems to resist tearing in the current. As a similar probable survival strategy, the capsules are almost sessile and the capsule wall is of many cell layers. *Scouleria* is especially obvious when dry because it forms jet-black mats on rocks exposed during late summer.

- A. Margin entire to apex; limbidium present as a one cell wide, unistratose border of enlarged and thicker-walled cells. B
- A. Margin serrate to dentate; margin mostly of several layers of cells, at least near leaf apex. C
- B. Median laminal cells smooth, quadrate, to 12 μm in diameter; leaves mostly less than 3 mm long. *Scopelophila cataractae*
- B. Median laminal cells papillose, hexagonal, >20 μm in diameter; leaves mostly more than 5 mm long. *Crumia latifolia*
- C. Distal leaf margin without enlarged cells; inframarginal limbidium not present in proximal portion of leaf. *Schistidium rivulare*
- C. One or several rows of cells of the distal leaf margin much enlarged and pellucid, often multi-stratose; at least the proximal portion of the leaf with a few abruptly elongate cells interior to the immediate leaf margin. D
- D. Capsules gymnostomous; leaf margin 3–5 cells thick above the leaf middle with internal cells of that thickened margin substereid. *Scouleria marginata*
- D. Capsules peristomate; leaf margin at most 2 cells thick without substereid cells internally. E
- E. Leaves bi- to multistratose in most of leaf; leaf shape somewhat ovate-lanceolate. *Scouleria* species A
- E. Leaves uniformly unistratose or with scattered bistratose streaks in the central lamina and on the margin; leaf shape elliptic, broadest near the middle. *Scouleria aquatica*

***Seligeria* Bruch & W. P. Schimper, 1846.**

Treated in this section are the smallest acrocarpous, epipetric mosses, none of which we have yet found in California. These mosses are so small as to become visible only when one looks across the edge of the rocks on which they are growing. They are too small to be easily seen without sporophytes, and so the key that follows primarily emphasizes sporophytic characters. The sporophytes are exserted on short but straight or arcuate setae. These plants grow exclusively on rocks but *Seligeria* is exclusively on calcareous substrates while *Brachydontium* is exclusively on siliceous substrates. The unrelated *Campylostelium* and *Tetradontium* are also keyed here because of their very small size.

Species included in this key: all Seligeriaceae, except *Campylostelium* (Ptychomitriaceae) and *Tetradontium* (Tetraphidaceae)

- Brachydontium olympicum* (E. Britton) McIntosh & Spence*
- Brachydontium trichodes* (Weber) Milde*
- Campylostelium saxicola* (Weber & D. Mohr) Bruch & W. P. Schimper*
- Seligeria campylopoda* Kindberg in Macoun*
- Seligeria donniana* (Smith) C. Müller Hal.*
- Seligeria recurvata* (Hedwig) Bruch & W. P. Schimper*
- Tetradontium brownianum* (Dickson) Schwägrichen*
- Tetradontium repandum* (Funck in Sturm) Schwägrichen*

Seligeria is recognizable primarily by the habitat. Calcareous seepages should be closely investigated for the extremely small plants of this genus. We expect that it will be found in some of the basaltic areas of the Modoc Plateau of northeastern California. Many of the springs which emerge from these lava plateaus are heavily charged with calcium bicarbonate which precipitates as small tufa deposits as the water emerges. These springs tend to be some of the most reliable places for calciphilous bryophytes in the state of California.

- A. Plant with an erect seta. B
- A. Plant with an arcuate seta. D
- B. Leaves with costa absent or ending before the apex; peristome teeth 4, rigidly erect; calyptra mitrate and lightly plicate. C
- B. Leaves with costa percurrent to excurrent in a narrow subula; peristome teeth 16 or absent; calyptra cucullate. E
- C. Perichaetial leaves costate to above middle, ovate and shortly acuminate, protonematal flaps to 2 mm long; flagelliform shoots present. *Tetradontium brownianum**
- C. Perichaetial leaves ligulate; ecostate; protonematal flaps to 0.5 mm long; flagelliform shoots frequent. *Tetradontium repandum**
- D. Capsule sulcate when mature and dry: plant on siliceous rocks, often granites or basalts. *Brachydontium trichodes**
- D. Capsule smooth when mature and dry; plant on calcareous seeps. *Seligeria donniana**
- E. Costa excurrent and filling up to 1/6 of the length of the leaf apex. *Seligeria recurvata**
- E. Costa percurrent in the mostly subulate apex. F
- F. Plant growing on calcareous seeps; leaves oblong-lanceolate, distally obtuse. *Seligeria campylopoda**
- F. Plant growing on siliceous rock, mostly only periodically moist; leaves narrowly subulate. G
- G. Seta shorter than the perichaetial leaves; capsule gymnostomous. *Brachydontium olympicum**
- G. Seta elevating capsule above the perichaetial leaves; capsule with 16 narrow peristome teeth. *Campylostelium saxicola**

Sematophyllum* Mitten, 1864. see *Hypnum

Sematophyllum adnatum (Michaux) E. Britton

Our only species of this largely tropical genus has been reported from *Eucalyptus* plantings in the city of San Francisco, and we believe it to be introduced. The genus *Sematophyllum* is a prostrate pleurocarpous and ecostate moss. The distinguishing character is the single row of 3–5 greatly enlarged and thin-walled cells at the alar angles.

***Sphagnum* Linnaeus, 1753.**

With nearly 200 species worldwide, *Sphagnum* covers large expanses especially in high latitudes, and it plays a dominant role in its ecosystem. Anyone working on bryophytes in temperate to polar regions should quickly become familiar with recognizing this genus. The features that should be emphasized in field recognition are the pale coloration, the fasciculate branching and the apical cluster of branches (capitulum). Among mosses, *Sphagnum* is the most economically utilized, and this is reflected in a number of field guides to the species in the genus.

Species included in this key: all Sphagnaceae

- Sphagnum angustifolium* (C. E. O. Jensen *ex* Russow) C. E. O. Jensen *in* Tolf*
- Sphagnum bartlettianum* Warnstorf
- Sphagnum capillifolium* (Ehrhart) Hedwig
- Sphagnum centrale* C. E. O. Jensen*
- Sphagnum compactum* Lamarck & A. P. de Candolle
- Sphagnum contortum* Schultz
- Sphagnum fallax* (Klinggräff) Klinggräff*
- Sphagnum fimbriatum* Wilson *in* W. J. Hooker
- Sphagnum fuscum* (W. P. Schimper) Klinggräff
- Sphagnum girgensohnii* Russow
- Sphagnum henryense* Warnstorf
- Sphagnum imbricatum* Hornschuch *ex* Russow*
- Sphagnum inundatum* Russow
- Sphagnum lescurii* Sullivant *in* A. Gray
- Sphagnum magellanicum* Bridel
- Sphagnum mendocinum* Sullivant
- Sphagnum palustre* Linnaeus
- Sphagnum papillosum* Lindberg
- Sphagnum platyphyllum* (Lindberg) Warnstorf
- Sphagnum quinquefarium* (Lindberg *in* Braithwaite) Warnstorf
- Sphagnum recurvum* Palisot de Beauvois*

- Sphagnum rubellum* Wilson*
- Sphagnum russowii* Warnstorf
- Sphagnum squarrosum* Crome in Hoppe
- Sphagnum strictum* Sullivant
- Sphagnum subnitens* Russow & Warnstorf
- Sphagnum subsecundum* Nees in Sturm
- Sphagnum tenellum* (Bridel) Bory*
- Sphagnum teres* (W. P. Schimper) Ångström in C. J. Hartman
- Sphagnum warnstorffii* Russow

Sphagnum is so distinctive as to resemble no other moss in the state. It follows that species identification of *Sphagnum* requires a very different suite of preparations from that done with other mosses. One must distinguish between the upright stem axis and its leaves and the branch axes with their leaves. With the stem axis, it is necessary to have a surface view of that axis after removing leaves and branches. It is also necessary to take a cross-section of that axis to determine the number of layers of thin-walled cortical cells outside of the thick-walled medulla (the wood cylinder). The stem leaves usually differ radically in shape and cellular morphology from the branch leaves. One finds the stem leaves by removing all the branches and then carefully removing one of the stem leaves (usually radically broader than the branch leaves). With the branch leaves, it is necessary to take a cross-section. Cross-sections are made holding down entire leafy branch axes and chopping sections from the constituent leaves by razor blade cuts across the entire leafy axis. In addition to the required branch leaf cross-sections, we require branch leaf whole-mounts and branch stems denuded of leaves.

Many of the characters used in *Sphagnum* refer to pores whose digestion patterns are genetically programmed. Similarly, larger portions of the cell walls of leaves, especially stem leaves, may be digested at maturity (resorbed). These pores and resorption areas, their size and arrangement, may be difficult to view without staining. Traditionally, crystal violet is used in such staining but the blue colors in a child's watercolor set work just as well. Simply take the moist and leafy stem or branch to a slide and put a droplet of stain on it prior to dissection and viewing.

Sphagnum in California is restricted to perennially saturated soils in bogs and fens—waterlogged sites that depend upon upwelling of perennially cold water. The distribution of each species seems to be relictual in that each of the California species is strongly discontinuous in distribution. *Sphagnum* has never been found with sporophytes in California.

- A. Cortical cells of stems and branches with spiral fibrils; apex of branch leaves concave and cucullate with abaxial surface appearing roughened by irregular digestion of the leucocyst walls. B
- A. Cortical cells of stem and branches without spiral fibrils; apex of branch leaves usually not cucullate. G
- B. Chlorocysts completely included within the layer of hyalocysts, or with slight and equal exposure of the lenticular chlorocysts on both surfaces. C
- B. Chlorocysts with a broad base of exposure on the adaxial surface, not exposed or only slightly exposed on the abaxial surface. D
- C. Plant typically with a reddish to copper blush. *Sphagnum magellanicum*
- C. Plant greenish to whitish green, never reddish tinged. *Sphagnum centrale**
- D. Chlorocysts mostly almost as broad on the adaxial surface as they are deep, thus appearing in cross-sections equilateral-triangular; leucocysts of stem leaves, especially near the leaf base, appearing once divided by an oblique fibrillose thickening of the cell wall. E
- D. Chlorocysts on adaxial surface markedly more narrow than deep, thus appearing in cross-sections isosceles-triangular; leucocysts of stem leaves without oblique fibrillae. F
- E. Chlorocysts, especially near the branch leaf bases, with abundant comb-fibrils; innermost walls of innermost layer of stem cortical cells horizontally striate. *Sphagnum imbricatum**
- E. Chlorocysts papillose on walls shared with leucocysts; cortical cells without horizontal striae. *Sphagnum papillosum*
- F. Hyalocysts of the branches with rounded-elliptic pores on the abaxial surface; chlorocysts, especially near the leaf base showing extensive development of comb-fibrils (seen as minute papillose roughenings of the lateral walls of those chlorocysts). *Sphagnum henryense*
- F. Hyalocysts of the branches with narrowly elliptic pores on the abaxial surface; chlorocysts without such comb-fibrils. *Sphagnum palustre*
- G. Cortical cells of branch stems isomorphic and distally porose (seen in branch cross-section as a single layer of uniform-sized enlarged outer cells); branch leaves truncate and denticulate at apex, much larger than the broadly deltoid stem leaves. H

- G. Cortical cells of branch stems dimorphic with only the larger ones porose (seen in branch cross-section as a layer of enlarged outer cells of two differing diameters); branch leaves usually narrowed and involute to an apex of varying shapes but not significantly truncate; branch leaves not much larger than the stem leaves. I
- H. Chlorocysts of branch leaves completely included; abaxial surface of hyalocysts of branch leaves with numerous pseudopores (ringed structures that resemble pores but lack digestion of actual holes). *Sphagnum compactum*
- H. Chlorocysts of branch leaves with broadest exposure on the abaxial surface; hyalocysts of branch leaves without pseudopores. *Sphagnum strictum*
- I. Chlorocysts of branch leaves with broadest exposure on the adaxial surface (look at and visually compare the chlorocysts of both surfaces of the leaf whole-mount). J
- I. Chlorocysts with broadest exposure on the abaxial surface, or with essentially equal or no exposure. S
- J. Stem leaves truncate or broadly rounded with distinct fimbriae across a distance equal to at least half the leaf width; central basal area of stem leaf with outer cell walls strongly resorbed forming a triangular, transparent and well demarcated central zone. K
- J. Stem leaves narrowed to apex, often notched but never fimbriate; central basal area of stem leaves without such a well demarcated central zone. L
- K. Stem leaves broadest near the apex, fringed across entire apex with the fringe often continuing even to the lateral margins. *Sphagnum fimbriatum*
- K. Stem leaves somewhat narrowed toward apex, fimbriate only in the central $\frac{1}{2}$ – $\frac{3}{4}$ of apex. *Sphagnum girgensohnii*
- L. Ascending branches mostly 3 per fascicle; stem leaves bordered below by elongate cells comprising over $\frac{1}{2}$ of leaf base, bordered above nearly to apex by a margin of elongate cells 3 or more cells wide. *Sphagnum quinquefarium*
- L. Ascending branches mostly 2 per fascicle; stem leaves more narrowly bordered. M
- M. Plant, especially the inner cells of the stem, brown, never red; plant forming very compact clones in bogs of low mineral availability; cortical cells of stem without pores (view a number of cells on stems stained with crystal violet). *Sphagnum fuscum*
- M. Plant with some reddish cast, or reddening when placed in dilute chlorox solution; clones rather loosely arranged; cortical cells of stem porose or not. N
- N. Stem leaves appearing acuminate to abruptly apiculate because of the strongly involute upper margins. O
- N. Stem leaves mostly with plane margins, or with margins not so much involute as to make the leaf apex appear narrowed. Q
- O. Leucocysts in median portions of branch leaves contacting the adjacent chlorocysts over only a small portion of their surface and thus hemispheric-convex on the abaxial surface; leaves of dry plant glossy. *Sphagnum subnitens*
- O. Leucocysts in median portions of branch leaves having a free convexity that describes less than 180° of arc; dry leaves not glossy. P
- P. Stem leaves more than 3:1; branch leaves noticeably 5-ranked; abaxial surface of proximal hyalocysts of stem leaves usually fibrillose throughout. *Sphagnum bartlettianum*
- P. Stem leaves less than 2.5:1; branch leaves not noticeably ranked; abaxial surface of proximal hyalocysts of stem leaves usually with membrane gaps. *Sphagnum capillifolium*
- Q. Hyaline cells in distal portion of branch leaves with ringed pores whose width is about $\frac{1}{5}$ of width of the cell; cortical cells of stem without pores. *Sphagnum warnstorffii*
- Q. Hyaline cells in distal portion of branch leaves with larger pores (mostly about $\frac{1}{5}$ of cell width) only obscurely ringed. R
- R. Cells of stem cortex mostly with pores; hyalocysts of stem leaves undivided, mostly short-rhomboidal. *Sphagnum russowii*
- R. Cells of stem cortex without pores; hyalocysts of stem leaves long rhomboidal, with cross-fibrils. *Sphagnum rubellum**
- S. Stem leaves mostly broadly triangular with the apex truncate, erose to nearly entire at apex; pores on abaxial portion of leucocysts of branch leaves to about $\frac{1}{5}$ of width of those leucocysts. T
- S. Stem leaves mostly ligulate, 3–4:1, quite lacerate at the apex; pores on abaxial portion of leucocysts of branch leaves mostly more than $\frac{1}{3}$ as broad as the leucocyst. U
- T. Branch leaves abruptly contracted to the squarrose limb; leucocysts with ringed pores on adaxial surface. *Sphagnum squarrosom*
- T. Branch leaves gradually contracted with the limb not usually strongly squarrose; leucocysts not ringed or inconspicuously so. *Sphagnum teres*
- U. Chlorocysts of branch leaves truncately elliptic with equal exposure on both surfaces; leucocysts

- of branch leaves with numerous small pores visible on the abaxial surface of the leaf, these pores strongly ringed and located at the junction of the spiral fibrils and the lateral cell margin; ascending and descending branches similar in length and degree of attenuation. V
- U. Chlorocysts of branch leaves triangular and exposed on dorsal surface; leucocysts mostly without so numerous commissural pores and often with those pores more centrally located over the lumen; descending branches significantly longer and more attenuate than the ascending ones. Z
- V. Stem cross-section showing 2–3 complete layers of enlarged and thin-walled cortical cells. W
- V. Stem cross-section showing a single layer of enlarged and thin-walled cortical cells. X
- W. Terminal bud protruding above capitulum and thus very obvious; stem leaves broadly elliptic, at least as large as branch leaves; ascending and descending branchlets of fascicle not clearly differentiated. *Sphagnum platyphyllum*
- W. Terminal bud inconspicuous within capitulum; stem leaves oblong to deltoid, smaller than branch leaves; ascending and descending branchlets of fascicle often somewhat differentiated. *Sphagnum contortum*
- X. Stem leaves mostly $\frac{1}{3}$ – $\frac{1}{2}$ as long as the branch leaves; hyalocysts of stem leaves mostly undivided. *Sphagnum subsecundum*
- X. Stem leaves mostly markedly more than $\frac{1}{2}$ as long as the branch leaves; hyalocysts of stem leaves mostly with several cross-fibrils. Y
- Y. Abaxial face of hyalocysts of stem leaves with numerous pores but with such pores few on the adaxial face. *Sphagnum lescurii*
- Y. Abaxial face of hyalocysts of stem leaves with few pores but with such pores numerous on the adaxial face. *Sphagnum inundatum*
- Z. Stem and branch leaves similar in size and shape and in cellular detail. *Sphagnum tenellum**
- Z. Stem and branch leaves quite dissimilar. AA
- AA. Branch leaf hyalocysts with pores on abaxial surface arranged in close rows along the commissures. *Sphagnum mendocinum*
- AA. Branch leaf hyalocysts without such a close commissural arrangement. AB
- AB. Stem leaves trapezoidal, truncate at the broad and fimbriate to dentate apex. *Sphagnum recurvum**
- AB. Stem leaves deltoid-triangular, about as broad as long, terminating in an acute to bluntly acute apex. AC
- AC. Branch leaves, when dry, strongly undulate, spreading at apices; capitula large and 5-radiate; stem leaves 0.7–1.1 mm long. *Sphagnum fallax**
- AC. Branch leaves, when dry, appressed, hardly undulate; capitula small, not conspicuously 5-radiate; stem leaves 0.4–0.8 mm long. *Sphagnum angustifolium**

Splachnum Hedwig, 1801. see *Tayloria*

- Splachnum ampullaceum* Hedwig*
- Splachnum sphaericum* Hedwig*
- Splachnum vasculosum* Hedwig*

Splachnum is one of the so-called dung mosses—a term given to a family of mosses that have evolved toward distribution of their spores by flies. We discuss much of the fly dispersal strategy in the section on *Tayloria*. In some respects, *Splachnum* is better adapted to fly dispersal because the hypophysis of the sporophyte is so broad as to form a parapet on which the flies can walk and pick up spores. It is so colorful that it might with careless observation be interpreted as a yellow or purple flower of a flowering plant. The sporophytes of *Splachnum* are usually so close together as to allow walking of flies from hypophysis to hypophysis.

Steerecleus H. Robinson, 1987. see *Euryhynchium*

Steerecleus serrulatus (Hedwig) H. Robinson

Steerecleus represents yet another recent generic segregate designed to bring unifying similarities to the species remaining in *Eurhynchium* and *Rhynchostegium*. The long rostrate operculum on this plant has justified its placement in the latter genus. It is discordant within that genus because of the lack of significant shortening of the distal cells of the leaf. The somewhat complanate leaf arrangement stands out among the plants of the *Eurhynchium* complex, as does the lack of significant alar differentiation.

Stegonia Venturi, 1883.

Mosses included in this section are very small, bulbiform, costate and concave-leaved plants with the costa percurrent to long excurrent. The distinguishing feature of *Stegonia* is seen in a leaf cross-section: the abaxial wall of each laminal cell is very thick while the adaxial wall is thin. Sporophytes in *Stegonia* can be sessile or exserted on a seta; they can be cleistocarpous or stegocarpous.

Species included in this key: all Pottiaceae

- Stegonia hyalinotricha* (Cardot & Thériot) Zander
- Stegonia latifolia* (Schwägrichen) Venturi ex Brotherus
- Stegonia pilifera* (Bridel) H. Crum & L. E. Anderson

Stegonia grows as individual plants but seldom as a monospecific turf. The plants are therefore very inconspicuous and seldom collected except when fertile. *Stegonia hyalinotricha* often grows among plants of the very similar *Phascum cuspidatum*. Under such circumstances, one can distinguish the *Stegonia* by the longer awn, as well as by the almost orbicular proximal leaves. These proximal leaves are produced early and usually wilt and fall off before sporophyte maturation. In the field, *S. latifolia* and *S. pilifera* will be confused with small species of *Tortula* but the more well developed peristome of *Tortula* should allow distinction from *Stegonia* with its very short and rather abortive peristome.

- A. Leaves with costa merely percurrent or excurrent in a short mucro. *Stegonia latifolia*
- A. Leaves with costa excurrent into a bleached to somewhat hyaline awn. B
- B. Median leaf cells papillose; awn bleached but not truly hyaline; capsule emergent on a long seta. *Stegonia pilifera*
- B. Median leaf cells smooth or nearly so; awn nearly hyaline; capsule sessile. *Stegonia hyalinotricha*

Straminergon Hedenäs, 1993. see *Calliergon*, *Hygrohypnum*

Straminergon stramineum (Dickson ex Bridel) Hedenäs

The single local species of *Straminergon* (previously placed in *Calliergon*) is a plant usually associated with *Sphagnum* in boggy sites. It is the only local plant with the combination of a costa extending above mid-leaf, a broadly rounded leaf apex, and a large alar group of inflated and thin-walled cells. The closely inserted, strongly overlapping distal leaves of the stems and branches form a bluntly acicular apex of each axis.

Syntrichia Bridel, 1801.

Syntrichia is one of a group of Pottiaceous mosses usually characterized by pluripapillose cells and C-shaped papillae. Mosses included in the genus *Syntrichia* have been viewed as part of the larger genus *Tortula*. Plants of *Syntrichia* are generally larger than those of *Tortula* but distinctions are made on the basis of costa cross-section morphology. Both genera have only an abaxial stereid band but that band is elliptic in *Tortula* but crescentic in *Syntrichia*. The abaxial face of the costa has an epidermis in *Tortula*—a feature lacking in *Syntrichia*.

Species included in this key: all Pottiaceae, except *Encalypta* (Encalyptaceae)

- Encalypta raptocarpa* Schwägrichen
- Syntrichia amplexa* (Lesquereux) Zander
- Syntrichia bartramii* (W. C. Steere in Grout) Zander
- Syntrichia bolanderi* (Lesquereux & T. P. James) Zander
- Syntrichia caninervis* Mitten
- Syntrichia laevipila* Bridel
- Syntrichia latifolia* (Bruch ex C. J. Hartman) Hübener
- Syntrichia norvegica* Weber
- Syntrichia obtusissima* (C. Müller Hal.) Zander
- Syntrichia pagorum* (Milde) Amann
- Syntrichia papillosa* (Wilson in Spruce) Juratzka
- Syntrichia papillosissima* (Coppey) Loeske
- Syntrichia princeps* (De Notaris) Mitten
- Syntrichia ruralis* (Hedwig) Weber & D. Mohr

Work with *Syntrichia* requires a stem cross-section preferably made within a few millimeters of the stem apex. It also requires a cross-section of a leaf made near leaf middle. The central strand in the stem

Tayloria W. J. Hooker, 1816.

Mosses included in this section have large median laminal cells with thin walls. The leaves usually are somewhat broadened above the middle, and most have serrate to dentate margins. The plants included here include all the members of the dung moss family (Splachnaceae), a family characterized by unusual modification of the neck of the capsule. Some Splachnaceae have that neck broadened into a parapet below the urn; others have the neck greatly elongated in a manner paralleled only in *Trematodon* in the unrelated family Bruchiaceae.

Species included in this key: all Splachnaceae, except *Oedipodium* (Oedipodiaceae)

- Oedipodium griffithianum* (Dickson) Schwägrichen*
- Splachnum ampullaceum* Hedwig*
- Splachnum sphaericum* Hedwig*
- Splachnum vasculosum* Hedwig*
- Tayloria hornschurchii* (Greville & Arnott) Brotherus*
- Tayloria lingulata* (Dickson) Lindberg*
- Tayloria serrata* (Hedwig) Bruch & W. P. Schimper*
- Tetraplodon mnioides* (Hedwig) Bruch & W. P. Schimper *

The family Splachnaceae is uniquely adapted to growing on high nitrogen substrates such as are afforded by dung and long decayed carcasses. Such habitats should be viewed as highly discontinuous in time and space. In the far north, such habitats are somewhat less discontinuous in time because of the slower rates of decay in such cold latitudes. However, at the latitude of California, dung and carcasses disappear too rapidly to support Splachnaceae except at very high elevations, and even high elevation sites only rarely will support members of the family. Members of the family Splachnaceae typically have spores distributed from source to appropriate target substrates by means of flies, and they have evolved toward sticky spores as an adaptation to such dispersal. Fly dispersal is effected because the chemicals contributed by decomposition become concentrated in the Splachnaceae sporophyte.

Sporophytes in the Splachnaceae are on erect setae often so close together as to allow walking of flies from one sporophyte to another. Most, and perhaps all, Splachnaceae are autoicous, and sporophytes are regularly to be expected. Identification of plants with sporophytes is easy based upon the greatly elongate or parapet-like hypophysis. When sterile, one looks for a *Bryum*-like plant (large thin-walled leaf cells on an acrocarpous plant). The leaves of western North American species of *Tayloria* are ligulate or spatulate, the rhizoids are smooth, and the axillary hairs have a somewhat clavate appearance due to the enlarged distal cell. Although the Splachnaceae are not yet known for California we expect that at least one species (*Splachnum*, *Tayloria* or *Tetraplodon*) will be found.

- A. Leaves very broadly spatulate with the broadened and rounded apex about 4 times as broad as the leaf base; margin of leaf base with long cilia. *Oedipodium griffithianum**
- A. Leaf apex not so much broader than the base; leaf margin not at all ciliate. B
- B. Leaf margins toothed to below the middle with at least some of the teeth multicellular. *Splachnum ampullaceum**
- B. Leaf margins entire to dentate but with those teeth not multicellular. C
- C. Leaves with apex rounded to obtuse at apex with costa ending before that apex; capsule erect with hypophysis more narrow than urn but as long or longer; calyptra fringed below with the individual lobes inwardly directed. D
- C. Leaves with apex acuminate to mucronate with costa length various; capsule various; base of calyptra not inwardly directed. F
- D. Leaves broadest near the middle, completely entire; columella exserted from mouth of urn. ... *Tayloria hornschurchii**
- D. Leaves broadest above the middle, entire to bluntly serrate. E
- E. Leaves with entire or nearly entire margins; urn above the apophysis not much longer than broad. *Tayloria lingulata**
- E. Leaves spatulate with bluntly serrate margins near the apices; urn above the apophysis about 1.5:1. *Tayloria serrata**
- F. Leaves lanceolate to oblanceolate abruptly contracted into a very narrow acumen; costa extending at least into the base of the acumen; hypophysis not broader than urn. *Tetraplodon mnioides**
- F. Leaves ovate to almost orbicular with apex mucronate to short acuminate; costa ending below the base of the mucro; hypophysis usually broadened relative to urn. G
- G. Leaf apex bluntly rounded or with a very short apiculus; margin mostly entire; hypophysis about twice as wide as urn. *Splachnum vasculosum**

- G. Leaf apex with a short or rather long acumen; margin mostly toothed with blunt teeth; hypophysis as wide as urn. *Splachnum sphaericum**

***Tetraphis* Hedwig, 1801.**

The mosses treated here are costate acrocarps with entire and plane-margined, almost orbicular leaves. The sporophytes are exerted on a straight or abruptly angular seta, and the capsules have only four triangular and rigidly erect peristome teeth. Older stems and leaves of *Tetraphis* have a brick-red wash completely recognizable once the field worker is properly introduced.

Species included in this key: all Tetraphidaceae

Tetraphis geniculata Girgensohn ex Milde*

Tetraphis pellucida Hedwig

In California, *Tetraphis* is a moss almost never found on any substrate except logs and stumps, and it seems restricted to the northwestern portion of the state. Its erect stems are usually crowned by a closely arranged series of reduced leaves that form a cup in which are found a cluster of elliptical gemmae. A novice might confuse this gemmae cluster of *Tetraphis* with that of *Aulacomnium androgynum*, also found on decaying wood, but usually on drier and more exposed wood. The easy differentiation is that *Tetraphis* has the gemma cluster subtended by the cup of modified leaves whereas the gemma cluster of *Aulacomnium* is without a subtending cup. One should also note possible confusion of these gemma cups with the splash-cup perigonia of such groups of plants as the Polytrichaceae, *Philonotis*, and *Pohlia*. The perigonia will show recognizable club-shaped antheridia at all stages of development—features radically different from the elliptical gemmae of *Tetraphis*.

- A. Seta smooth and erect; plant common on logs and stumps throughout moist areas of the state. *Tetraphis pellucida*
 A. Seta bent at about its middle with obvious papillosity at least at that bend; plant very rarely encountered but growing in habitats similar to the previous species. *Tetraphis geniculata**

Tetraplodon* Bruch & W. P. Schimper, 1844. see *Tayloria

Tetraplodon mnioides (Hedwig) Bruch & W. P. Schimper*

Tetraplodon mnioides is one of the most common Splachnaceae in states to the north of California. This species is unusual in the family in tolerating mesic as well as water-logged conditions of the substratum. It is regularly found on owl pellets on boulder perches along trails in lowland moist forests near the coast in Washington State. *Tetraplodon* is easily distinguished from *Tayloria* and *Splachnum* on the basis of its ovate-lanceolate (not obovate or spatulate) leaves, and on the basis of its hypophysis that is about as wide as the urn above.

Tetradontium* Schwägrichen, 1824. see *Seligeria

Tetradontium brownianum (Dickson) Schwägrichen*

Tetradontium repandum (Funck in Sturm) Schwägrichen*

Tetradontium usually grows in dimly lit positions on the ceilings of rock overhangs. It is very small, and it grows as scattered plants rather than as a monospecific turf. In general the only fully developed leaves are the perichaetial bracts, and much of the photosynthesis is done by thallose flaps of protonematal origin. The capsules on these extremely small plants are diagnostic: four erect, cellular peristome teeth, and a lightly plicate calyptra.

Thamnobryum* Nieuwland, 1917. see *Neckera

Thamnobryum neckeroides (W. J. Hooker) E. Lawton

Thamnobryum (with *Climacium* and *Leucolepis*) is one of our three truly dendroid mosses. In California, it seems almost restricted to soil in high montane coniferous forests, and in high elevation *Alnus* thickets. A quick hand-lens look at the leaves of this plant is sufficient for identification: blunt leaves, no limbidium, short cells of the median lamina.

Thuidium* Bruch & W. P. Schimper, 1852. see *Hylocomium

Thuidium recognitum (Hedwig) Lindberg*

Thuidium is common and species diverse in the eastern United States as well as in most of the Northern

Hemisphere. Its absence from western North America is nearly complete except for an arc of distribution that extends from eastern North America into the high Arctic thence southward in the mountains of Alaska and British Columbia barely reaching Washington State. The stems of *Thuidium recognitum* are several times pinnately branched and have dense, branched and filamentous paraphyllia. As such, *Thuidium* could be confused only with *Hylocomium splendens*. *Thuidium* differs from the latter species in many respects and can be differentiated immediately by experienced persons. Objective differences include the single costa of *Thuidium* (not double and branching from the base) and the central papillosity (not prorate).

***Timmia* Hedwig, 1801.**

Mosses presented in this section are acrocarpous and costate plants with stiff leaves somewhat reminiscent of members of the Polytrichaceae. *Timmia* is readily recognized by the sheathing base of every leaf. That leaf base is so radically different in color and orientation and is so closely wrapped around the stem that it may initially be misinterpreted as simply part of the stem.

Species included in this key: all Timmiaceae

- Timmia austriaca* Hedwig
- Timmia bavarica* Hessel.
- Timmia megapolitana* Hedwig*

The special character of leaf sheath differentiation allows *Timmia* to be confused only with *Bartramia ithyphylla*. That species of *Bartramia* and the three species of *Timmia* should be examined in the field by pulling a single leaf down and off the stem. Such a pulling action will remove the leaf exposing the sheathing base that completely surrounds the stem. This sheathing base is precisely defined in that the contraction to the leaf limb is so abrupt as to completely define the sheath as opposed to the leaf limb. Fully hydrated larger specimens of *Timmia* may be confused in the field with a Polytrichaceae but the photosynthetic lamellae of that family show as longitudinal lines of more intensively green-pigmented cells even under a hand-lens. *Timmia*, when dry, may resemble in the field such highly crispate, plane-margined mosses as *Trichostomum*. However, if a *Timmia* leaf is carefully folded between one's fingers so as to view under a hand-lens across the adaxial surface of the leaf, the large single mammillae of each leaf cell of *Timmia* will appear as a contrast to the multiple papillae of *Trichostomum* and its allies.

- A. Leaf sheath orange to brown, lacking stereids in cross-sectional view; cilia of endostome not appendiculate; plant dioicous. *Timmia austriaca*
- A. Leaf sheath hyaline to cream-colored, with stereids; cilia appendiculate; plant monoicous. B
- B. Distal portion of leaf sheath with papillose cells; median cells of the limb mostly more than 10 μm in diameter; cells with corner thickenings; basal membrane of endostome with apertures. *Timmia megapolitana**
- B. Distal portion of leaf sheath smooth; median cells of the limb mostly less than 10 μm; cells without corner thickenings; basal membrane of endostome without apertures. . . . *Timmia bavarica*

***Timmiella* (De Notaris) Limpricht in Rabenhorst, 1888.**

Mosses included in this section are plane margined acrocarps dentate near the leaf apices, and high mammillose on the adaxial leaf surface. The leaves are strongly crispate when dry and, in that condition, the pearly white costa seems of radically different coloration from the adjacent leaf.

Species included in this key: all Pottiaceae

- Timmiella anomala* (Bruch & W. P. Schimper) Limpricht
- Timmiella crassinervis* (Hampe) L. Koch

Timmiella is readily recognized in the field by the combination of plane leaf margins, crispate and opaque leaves (a product of the high mammillose adaxial cells of the bistratose lamina). Determination of the plant to species may, however, be quite difficult. Plants with sporophytes are easily determined by the straight peristome teeth of *Timmiella crassinervis* as opposed to the spirally twisted exostome of *Timmiella anomala*. Unfortunately neither species of *Timmiella* has sporophytes in any frequency. Even gametangia will often be difficult to find and so the monoicous sexual condition of *Timmiella anomala* may be difficult to determine. Without great conviction, we include in the key below the character of leaf base definition—a character mentioned by Crum and Anderson (1981). When sporophytes allow determination, we have found that plants from the humid northwest of the state are usually *Timmiella crassinervis* while plants from the drier half of the state are usually *Timmiella anomala*. *Timmiella* is almost restricted to seasonally dry mineral soil, usually clayey, often on eroded banks.

- A. Leaf bases markedly broader than limb with the contraction to that limb rather abrupt; peristome and exothecial cells of operculum not twisted; plant dioicous. *Timmiella crassinervis*
- A. Leaf bases hardly broader than limb with no definition of shoulders at base-limb junction; peristome and exothecial cells of operculum twisted about one full spiral; plant monoicous.
. *Timmiella anomala*

Tomentypnum* Loeske, 1911. see *Homalothecium

Tomentypnum nitens (Hedwig) Loeske*

Tomentypnum, along with other strongly plicate, costate pleurocarps, has traditionally been placed in a much expanded *Homalothecium*. The recent work of Hedenäs, however, requires placement in the Campyliaceae along with a large number of other aquatic and semi-aquatic mosses. In the Campyliaceae, *Tomentypnum* joins *Conardia* as one of the two local mosses that produce rhizoids from cells along the abaxial face of the costa. The rhizoids of *Tomentypnum* are so regularly present as to allow the use of that character as a main diagnostic feature. The much smaller plant *Conardia* only occasionally has rhizoids inserted on its costa, and this latter genus has papillose rhizoids compared with the smooth rhizoids of *Tomentypnum*. The feature of rhizoids inserted on the costa should be distinguished from that of nematogons on distal portions of leaves (a common feature of many other Campyliaceae). When it is stated that nematogons are present on leaves we are referring to rhizoid initials in the leaf lamina itself rather than on the surface of the costa. *Tomentypnum*, not yet known from the state, should be found in bogs and fens of calcareous areas such as the Marble Mountains of northwestern California.

Tortella* (Lindberg) Limpricht, 1888. *nomen conservandum

Mosses treated in this section are densely papillose acrocarpous plants with plane leaf margins and with strongly differentiated basal cells, usually thin-walled and rectangular. The basal cells extend up the leaf margin so that such thin-walled and rectangular, smooth cells border the actual shoulder of the leaf.

Species included in this key: all Pottiaceae

- Oxystegus tenuirostris* (W. J. Hooker & Taylor) A. J. E. Smith
- Tortella alpicola* Dixon
- Tortella fragilis* (W. J. Hooker & Wilson in Drummond) Limpricht
- Tortella tortuosa* (Hedwig) Limpricht

In California, this is one of the easiest genera of the Pottiaceae to recognize. Our three species are rather large mosses in compact cushions. In California, two of our *Tortella* have undistorted and fragile leaves; the other has leaves so crispate that they seem to tangle with one another. Under the microscope, the hyaline and rectangular cells of the leaf base ascend up the leaf margin in such a well demarcated zone as to create a V-shaped line between the cells of the base and those of the limb.

Our species of *Tortella* are primarily calciphiles, and the scarcity of such habitats in montane California accounts for the few collections of species of this genus.

- A. Leaves gradually contracted into a narrowly linear to subulate apex. *Tortella tortuosa*
- A. Leaves broader at the apex with the costa mucronate. B
- B. Leaves strongly crispate when dry, often losing portions of their lamina but not with broken apices; differentiated basal cells extending barely to the shoulders and thus not defining a V-shaped line between the basal cells and those of the limb. *Oxystegus tenuirostris*
- B. Leaves rigid, usually with many of the apices broken; differentiated basal cells extending above the shoulders and thus defining a V-shaped line between the basal cells and those of the limb. . . . C
- C. Leaf bases strictly hyaline, without a yellowish blush; distal portion of leaves segmented into a series of elliptical and multicellular segments; leafy stems with rhizoids not formed into a dense indumentum; stems with central strand. *Tortella alpicola*
- C. Leaf base usually with a yellowish blush; distal portion of leaves not articulated but instead breaking into segments of irregular lengths; leafy stems with rhizoids often densely compacted into axillary indumenta; stem without central strand. *Tortella fragilis*

***Tortula* Hedwig, 1801.**

The concept of the genus *Tortula* has changed radically in recent years as a result of the monumental work of Dr. Richard Zander. The newly circumscribed *Tortula* can be defined on the basis of broad,

usually ovate to elliptic or obovate, leaves. The costal cross-section has a single abaxial stereid band, and most species have clear epidermis on both surfaces of the costa.

Species included in this key: all Pottiaceae

- Hennediella heimii* (Hedwig) Zander
- Hennediella stanfordensis* (W. C. Steere) Blockeel
- Leptophascum leptophyllum* (C. Müller Hal.) J. Guerra & M. J. Cano
- Pseudocrossidium crinitum* (Schultz) Zander
- Tortula atrovirens* (J. E. Smith) Lindberg
- Tortula brevipes* (Lesquereux) Brotherus
- Tortula californica* E. B. Bartram
- Tortula euryphylla* Zander
- Tortula guepinii* (Bruch & W. P. Schimper) Brotherus
- Tortula inermis* Bridel
- Tortula leucostoma* (R. Brown) W. J. Hooker & Greville
- Tortula mucronifolia* Schwägrichen
- Tortula muralis* Hedwig
- Tortula nevadensis* (Cardot & Thériot) Zander*
- Tortula obtusifolia* (Schwägrichen) Matthieu
- Tortula plinthobia* (Sullivan & Lesquereux in A. Gray) Brotherus
- Tortula protobryoides* Zander
- Tortula subulata* Hedwig
- Tortula systylia* (W. P. Schimper) Lindberg
- Tortula truncata* (Hedwig) Mitten in Godman

Most of the larger sized members of the genus are now placed in the genus *Syntrichia*. Two genera of rather small plants, *Desmatodon* and *Pottia* are either not now recognized or have had many of their members transferred into the genus *Tortula*. *Phascum* is a genus of small mosses with sessile and cleistocarpous capsules but with leaf morphology similar to that of many species of *Tortula*. Zander incorporated the genus *Phascum* into *Tortula* but we prefer to recognize *Phascum*.

- A. Hyaline point consistently absent; sometimes mucronate to apiculate or with a few enlarged apical cells. B
- A. Hyaline point present on at least some leaves. M
- B. Leaf cells smooth to mammillose, or with a few small papillae in distal portion of leaf; cells of leaf margin typically somewhat smaller and thicker walled than adjacent laminal cells. C
- B. Leaf cells papillose, usually densely so; margin various. F
- C. Costa cross-section showing no stereid band or with only 1–4 such dorsal stereid cells; cells of leaf middle thin and bulging-vesiculose; margin crenulate-papillose. *Leptophascum leptophyllum*
- C. Costa cross-section showing a clear dorsal stereid band; cells of leaf middle with somewhat thickened walls, not vesiculose; leaves entire or low dentate near the apex. D
- D. Leaf margins strongly recurved to revolute at least near base; plants mostly with stems more than 5 mm long with leaves conduplicate folded when dry. *Tortula mucronifolia*
- D. Leaf margins plane throughout; plants mostly smaller with leaves crumpled when dry. E
- E. Leaf margins entire throughout; peristome absent; deoperculate capsule hemispheric or nearly so. *Tortula truncata*
- E. Leaf margins on well developed leaves with a few serrulations near the apices; peristome present; deoperculate capsule short cylindric, mostly about 2:1. *Tortula nevadensis**
- F. Leaf bordered by elongate cells to above the middle. G
- F. Leaf not bordered by elongate cells, or border restricted to leaf base. H
- G. Leaves mostly more than 3 mm long with entire or papillose-crenulate margins; plant autoicous and usually with sporophytes. *Tortula subulata*
- G. Leaves little more than 1 mm long with at least a few marginal cells enlarged into teeth; plant dioicous, unknown with sporophytes. *Hennediella stanfordensis*
- H. Plants with a thick cushion of enlarged cells on the ventral surface of the costa at the distal end; plants of periodically dry soil in arid areas. *Tortula atrovirens*
- H. Ventral surface of costa plane or grooved, not convex. I
- I. Leaves deeply concave, rather closely comose, appearing somewhat bulbiform; leaf apex acuminate; capsules cleistocarpous. *Tortula protobryoides*
- I. Leaves not forming a strongly bulbiform cluster; leaf apex obtuse to mucronate; capsules ste-gocarpous. J

- J. Marginal cells throughout upper and median portion of leaf epapillose or nearly so, radically differentiated from the heavily papillose interior cells. *Hennediella heimii*
- J. Marginal cells not differentiated from interior laminal cells. K
- K. Leaves folded lengthwise and variously twisted when dry. *Tortula inermis*
- K. Leaves little distorted when dry. L
- L. Median leaf cells typically less than 12 μm in diameter; plant of soil banks in lowland oak savannahs and grasslands. *Tortula obtusifolia*
- L. Median leaf cells typically more than 15 μm ; plant of wet soils in high montane regions. *Tortula euryphylla*
- M. Leaf cells typically smooth. N
- M. Leaf cells papillose, usually densely so. O
- N. Capsule systylious and with peristome short, not much spirally twisted; leaf cells mostly 2:1, to 20 μm long. *Tortula systylia*
- N. Capsule with operculum free from the columella; peristome long and twisted in several spirals; leaf cells nearly isodiametric, mostly over 25 μm wide. *Tortula californica*
- O. Leaves bordered with thicker-walled cells or marginal cells with corner-thickenings; plant epiphytic or on cement or brick walls. *Tortula muralis*
- O. Leaves not so bordered; plant of calcareous or desert soil. P
- P. Marginal cells more lightly papillose than adjacent cells; leaves seldom more than 1.5 mm long; plant mostly on periodically dry lowland soils near the coast. *Tortula guepinii*
- P. Marginal cells not more lightly papillose; leaves mostly more than 2 mm long. Q
- Q. Leaves, disregarding the awn, narrowed to apex, usually acute. R
- Q. Leaves, disregarding the awn, rounded to emarginate at apex. S
- R. Leaves broadest near the base; juxtalaminar, abaxial cells of costa usually enlarged and yellowish-brown to orange in a pair of uniseriate rows on each side of costa; marginal recurvature at least at mid-leaf performing a complete spiral. *Pseudocrossidium crinitum*
- R. Leaves ovate to ovate-lanceolate, broadest at or near the middle, juxtalaminar, abaxial cells of costa not so differentiated; marginal recurvature less pronounced. *Tortula leucostoma*
- S. Median cells mostly more than 15 μm broad; plants of rather moist habitats at high elevations; dry leaves weakly crispate, not at all carinate. *Tortula euryphylla*
- S. Median cells mostly smaller; plants of lower elevations; dry leaves weakly carinate, mostly twisted around stem. T
- T. Awn mostly less than 2 mm long with leaves often simply mucronate; mucro or awn irregularly low serrulate near apex; peristome without a basal membrane. *Tortula plinthobia*
- T. Awn mostly about 4 mm long with that awn entire or nearly so; peristome with filiform teeth arising from a clear basal membrane. *Tortula brevipes*

Trachybryum* (Brotherus) W. B. Schofield, 1968. see *Homalothecium*, *Hylocomium

Trachybryum megaptilum (Sullivant) W. B. Schofield

Trachybryum is the only species of a genus endemic to the west coast of North America. It is a segregate from the pleurocarpous genus *Homalothecium* with which it shares the features of plicate leaves and a strong costa. *Trachybryum* was segregated from *Homalothecium* on the basis of the elongate (not quadrate) cells of the alar region. Additional differential characters include the plumose growth pattern from a somewhat upwardly directed main stem axis. The leaves are broadly ovate rather than variously lanceolate as in *Homalothecium*, and the median cells are very strongly porose.

Trachybryum megaptilum is one of several species of moss that have been called “pseudautoicous” on the basis of the presence of dwarf males in the axils of leaves very near the perichaetia. Such dwarf males arise from separate spores which fall into those leaf axils and grow into structures consisting of nothing more than a very short stem without vegetative leaves but with perigonal leaves surrounding a group of antheridia and paraphyses.

Trematodon* Michaux, 1803. see *Bruchia

Trematodon boasii W. B. Schofield

Trematodon is a moderately large genus widely distributed throughout the world. However, it has only recently been found in California. *Trematodon boasii* was first found on Vancouver Island in British Columbia but it has recently been discovered at high elevations in the Central Oregon Cascades. It is a plant of moist soil in high montane and alpine regions. It is so small that it is unlikely to be collected

except when sporophytes are present. The sporophytes are rigidly erect with a hypophysis somewhat longer than the urn. The gametophyte has leaves about 2 mm long with a strongly defined subula above a clasping and broadened leaf base.

Trichodon* W. P. Schimper, 1856. see *Ditrichum

Trichodon cylindricus (Hedwig) W. P. Schimper

Trichodon is a genus segregated from the acrocarpous and subulate leaved *Ditrichum*. The basis for this segregation lies in the strongly expanded leaf base that allows for the clasping base to be distinguished from the squarrose leaf limb. The subula of *Trichodon* is more papillose-prorate than most species of *Ditrichum*. Like most species of *Ditrichum*, *Trichodon* has plane to basally incurved leaf margins. It is found on muddy road or trail banks primarily in the northwestern portions of California. Sporophytes have not been seen on *Trichodon* in California, and this may account for the scarcity of its collection.

Trichostomum* Hedwig, 1801. see *Weissia

Trichostomum brachydontium Bruch in F. A. Mueller

Trichostomum crispulum Bruch in F. A. Mueller

Trichostomum sweetii (E. B. Bartram) Stark

Plants assigned to *Trichostomum* generally are larger than those placed in *Weissia*, and the leaf margins are plane rather than incurved. With *Oxystegus* and *Tortella*, we have a group of four closely related genera differing only by a suite of characters without any one of those characters definitive. *Oxystegus* and *Tortella* are generally plants with rather flexuose or fragile leaves; *Trichostomum* and *Weissia* have rather stiff but often crispate leaves, perhaps a function of the generally shorter proportions of their leaves. The leaves of *Trichostomum* are generally with plane margins while those of *Weissia* are generally incurved.

Tripterocladium* A. Jaeger, 1880. see *Lescuraea

Tripterocladium leucocladulum (C. Müller Hal.) A. Jaeger

Tripterocladium, throughout its range, is very unpredictable as to site of occurrence with each of its occurrences south of the Canadian border representing a considerable disjunction of range. In the field, *Tripterocladium* resembles a very small *Pterigynandrum* but it has smooth rather than prorate cells. *Tripterocladium* is known in California from a single Siskiyou County collection.

Triquetrella* C. Müller Hal., 1897. see *Didymodon

Triquetrella californica (Lesquereux) Grout

Our one species of *Triquetrella* is a plant of near-the-ocean sites from central Oregon to southern California. It is readily recognized even in the field by the combination of tristichous and papillose lanceolate leaves with broad and obvious decurrencies. The type of *Triquetrella californica* is reported as having been collected by Henry Bolander on Mt. Diablo in Contra Costa Co., California but we have been unable to find the plant in repeated collecting trips to that area. Most occurrences of *Triquetrella* have been located within ten miles of the ocean. In such ocean-front areas, careful examination of areas immediately downslope to outcropping boulders in coastal grasslands are the most promising locations for finding *Triquetrella*. Based on its preferred habitat coupled with increasing urban development of coastal California counties, the few remaining occurrences of *T. californica* suggest that it is among the most threatened species of mosses in the state.

Ulota* D. Mohr, 1806. see *Orthotrichum

Ulota is restricted in California to the humid forests and coastline in extreme northwestern portions of the state. Our species are strongly crispate plants which share with *Orthotrichum* an ecthydic life strategy: they very rapidly take in water that falls on any portion of their plant, and they lose water to evaporation at similar rates. A droplet of water placed on a dry plant of either genus causes immediate squirming of that plant as the leaves absorb the water. As a member of the Orthotrichaceae, *Ulota* has hairy calyptrae and somewhat sulcate capsules. The plants in this genus differ from *Orthotrichum* in having leaves with one or several rows of isodiametric marginal cells in the alar regions.

Species included in this key: all Orthotrichaceae

Ulota megalospora Venturi in Röhl

Ulota obtusiuscula C. Müller Hal. & Kindberg in Macoun

Ulota phyllantha Bridel
Zygodon rupestris W. P. Schimper ex Lorentz

Ulota is primarily a plant of more humid climates than those of *Orthotrichum*. Like those *Orthotrichum* that occupy more humid habitats (*O. pulchellum* and *O. consimile*), *Ulota* is generally quite crispate, and has superficial stomates. Our three species of *Ulota* differ radically in habitats. *Ulota phyllantha* is a plant of twigs and rocks within a few miles of the ocean shore in northwestern California. *Ulota obtusiuscula* is a plant of twigs and trunks in northwestern California, always in perpetually humid regions. *Ulota megalospora* is a plant of tree canopies, especially conifers. It can be predicted when one encounters a ridge-top *Pseudotsuga* with a large horizontally-oriented branch and, in such sites, it will be on the underside of the branch.

- A. Apex of upper leaves with a reddish-brown cluster of septate gemmae; plant found only within a mile or so of the ocean. *Ulota phyllantha*
- A. Apex of leaves not gemmiparous; plant more widely distributed. B
- B. Apex of leaf not uniseriate; plant forming tight cushions of strongly crispate leaves. *Ulota obtusiuscula*
- B. Apex of leaf filiform with about 2–5 isodiametric to short-rectangular cells in a uniseriate apex. . . . C
- C. Plant tufted with rhizoids axillary and bearing abundant multicellular elliptical gemmae. *Zygodon rupestris*
- C. Plant stoloniferous with prostrate axes possessing abundant red-brown rhizoids, gemmae absent. *Ulota megalospora*

Vesicularia* (C. Müller Hal.) C. Müller Hal., 1896. see *Hypnum

Vesicularia vesicularis (Schwägrichen) Brotherus

Vesicularia is occasionally introduced as a lawn weed into California, especially in the area of San Francisco. It is a very non-descript plant notable for complanate leaves with very large cells and with very little differentiation of an alar region. It would most likely be confused for *Plagiothecium* but the presence of filamentose pseudoparaphyllia, non-decurrent leaves and the lack of an hyaloderm contradict such an assumption. The median laminal cells are short hexagonal with cell width mostly more than 20 µm, much broader and relatively shorter than any *Plagiothecium*.

Warnstorfia* Loeske, 1907. see *Drepanocladus

The plants in this section are aquatic pleurocarps, especially in bogs and fens. The plant has a costa that extends into the acumen or beyond, and the leaves are usually falcate-secund.

Species included in this key: all Campyliaceae

Warnstorfia exannulata (Bruch & W. P. Schimper) Loeske
Warnstorfia fluitans (Hedwig) Loeske

Warnstorfia is becoming more commonly recognized as a segregate of the larger genus *Drepanocladus*. This latter genus has traditionally been the name for aquatic and pleurocarpous mosses with falcate-secund, narrow leaves and strong costae ending in the leaf acumen. Tuomikoski & Koponen (1979) asserted that *Drepanocladus* is a phylogenetically diverse grouping that demanded breakup into a number of additional genera. *Warnstorfia* is distinguished as plants radially (rather than planar) branched with serrulate leaf margins, with a strongly differentiated group of thin-walled and inflated alar cells. The leaf apices have a few somewhat enlarged and seemingly empty cells that function as nematogons. Unlike *Drepanocladus sensu stricto*, *Warnstorfia* has the capacity to produce reddish pigmentation in the leaves, especially in sites with strong insolation. Our two species of *Warnstorfia* are more generally found in flowing water while *Drepanocladus* is often in still water.

- A. Alar cells inflated and extending in a transversely triangular group nearly or completely across the leaf base; partial hyalodermis distinguishable as a layer of outer cells somewhat larger and thinner walled than adjacent interior ones pseudoparaphyllia often broader than long; plant dioicous. *Warnstorfia exannulata*
- A. Alar cells restricted to a small pocket in the alar angles, seldom extending to the costa; hyalodermis not distinguishable; pseudoparaphyllia lanceolate; plant autoicous. . . . *Warnstorfia fluitans*

Weissia Hedwig, 1801.

Mosses included in this section are acrocarpous mosses with crispate leaves and densely papillose median laminal cells. The leaves have plane to incurved leaf margins and those margins are entire or nearly so.

Species included in this key: all Pottiaceae

- Oxystegus tenuirostris* (W. J. Hooker & Taylor) A. J. E. Smith
- Plaubelia sprengelii* (Schwägrichen) Zander*
- Trichostomum brachydontium* Bruch in F. A. Mueller
- Trichostomum crispulum* Bruch in F. A. Mueller
- Trichostomum sweetii* (E. B. Bartram) Stark
- Weissia andersoniana* Zander
- Weissia andrewsii* E. B. Bartram
- Weissia condensa* (Voit in J. W. Sturm) Lindberg
- Weissia controversa* Hedwig
- Weissia inoperculata* (H. Crum) H. Crum, W. C. Steere & L. E. Anderson
- Weissia ligulaefolia* (E. B. Bartram) Grout
- Weissia planifolia* Dixon*
- Weissia sinaloensis* E. B. Bartram*

Weissia is readily recognized in the field by the combination of the small size, opaque leaves (a product of the dense papillae), plane to incurved leaf margins and generally mineral soil habitat. The most common species, *W. controversa*, is one of the most widespread mosses on disturbed soil of cultivations or of bare patches of soil in lawns. We have decided not to recognize the genus *Hymenostomum*. This has been separated from *Weissia* on the basis of a peristome reduced to a simple membrane. Members of this segregate (see *W. inoperculata*) may even have the operculum separating tardily, if at all, from the urn. Many species of *Weissia* in California reside in the deserts.

- A. Leaf margins plane to erect when moist. B
- A. Leaf margins incurved when moist. F
- B. Hyaline, rectangular cells of the leaf base extending to shoulder, and thus reaching somewhat farther along the margins than along the costa; upper portion of leaf lamina tending to be quite fragile and separating from the leaf in small pieces. *Oxystegus tenuirostris*
- B. Hyaline, rectangular cells of the leaf base not extending to shoulder; upper portion of leaf lamina not fragile. C
- C. Leaves minutely mucronate to rounded at apex, mostly less than 2 mm long, typically with costa only 3–4 cells wide at mid-leaf. D
- C. Leaves cucullate or mucronate-recurved at apex, mostly more than 2 mm long, typically with costa 5–6 cells wide at mid-leaf. E
- D. Leaves broadest near the middle. *Weissia sinaloensis**
- D. Leaves ligulate with parallel sides. *Weissia planifolia**
- E. Leaf apices with a short and reflexed mucro; leaf base with the rectangular cells only gradually demarcated from the quadrate cells of the mid-leaf. *Trichostomum brachydontium*
- E. Leaf apices channeled and somewhat cucullate; leaf base with the rectangular cells abruptly demarcated from the quadrate cells of the median leaf lamina. *Trichostomum crispulum*
- F. Cells with high and branched papillae that arise from a mammillose cell lumen; leaves with limb constricted above junction with differentiated basal cells. *Weissia andersoniana*
- F. Papillae low and unbranched, mostly not arising from a mammillose cell lumen; leaves not strongly constricted at base of limb. G
- G. Median leaf cells bulging mammillose on adaxial surface, smooth and flat abaxially; papillae low to absent; leaf incurvature loose and broad, not extending to leaf apex. *Plaubelia sprengelii**
- G. Median leaf cells not bulging mammillose, mostly strongly papillose; leaf incurvature tight and narrow, extending to near leaf apex. H
- H. Costa mostly less than 50 μ m wide at base. I
- H. Costa 60–90 μ m wide at the base. K
- I. Leaves broadest below the middle; apex acute to narrowly obtuse or mucronate. *Weissia controversa*
- I. Leaf base ligulate with parallel sides, mostly with the more elongate cells extending farther along costa than along margin. J
- J. Leaf apex acute above the inrolled margin; capsule cleistocarpous. *Weissia inoperculata*
- J. Leaf apex broadly acute to rounded; capsule stegocarpous. *Weissia ligulaefolia*

- K. Margin at mid-leaf inrolled in nearly a complete spiral. *Weissia andrewsii*
- K. Margin at mid-leaf incurved but not so much inrolled. L
- L. Leaves ligulate, with essentially parallel margins. *Trichostomum sweetii*
- L. Leaves narrowly ovate-lanceolate, broadest near the base. *Weissia condensa*

Zygodon* W. J. Hooker & Taylor, 1818. see *Gymnostomum*, *Orthotrichum

In the key that appears below we deal with a pair of very different plants traditionally considered congeneric. Both are acrocarpous plants with entire leaf margins, and with dense clusters of multicellular rhizoidal gemmae in the axils of keeled leaves. Sporophytes are uncommon but both species have sulcate, gymnostomous capsules exerted on short setae.

Species included in this key: all Orthotrichaceae

Zygodon menziesii (Schwägrichen) Arnott

Zygodon rupestris W. P. Schimper ex Lorentz

Only a single species of *Zygodon* seems to be native to California, but several recent collections of the austral *Zygodon menziesii* have been gathered from the bark of planted trees within the city of San Francisco. This genus belongs in the Orthotrichaceae but the two species are very different. The native *Z. rupestris* combines pluripapillose cells and plane leaf margins with the result that it may be placed near the Pottiaceous genus *Gymnostomum*. In contrast, *Z. menziesii* has smooth leaf cells and basally recurved leaf margins. Both species, however, have the Orthotrichaceae characteristic of rapid water uptake when moistened.

Throughout the world the genus *Zygodon* can usually be identified by the densely placed elliptical and multicellular axillary gemmae. *Zygodon rupestris* is widespread, especially on *Quercus*, in the more humid regions of lowland coastal areas of the state.

- A. Leafy stems hamate when dry, not significantly spirally twisted; median leaf cells pluripapillose; leaves ending in a uniseriate apex. *Zygodon rupestris*
- A. Leafy stems not at all hamate at apices but with leaves clockwise twisted around stem when dry; all cells of leaf smooth; leaf apices obtuse to blunt. *Zygodon menziesii*

APPENDIX I.

SUPRAFAMILIAL ARRANGEMENT OF THE FAMILIES OF CALIFORNIA MOSSES (MODIFIED FROM BUCK AND GOFFINET 2000)

Genera with an asterisk (*) are not yet known from California despite occurrence in nearby states.

Class Sphagnopsida

Order Sphagnales

Family Sphagnaceae (*Sphagnum*)

Class Andreaeopsida

Order Andreaeales

Family Andreaeaceae (*Andreaea*)

Class Polytrichopsida

Order Tetraphidales

Family Tetraphidaceae (*Tetraphis*, *Tetradontium**)

Family Oedipodiaceae (*Oedipodium**)

Family Buxbaumiaceae (*Buxbaumia*)

Order Polytrichales

Family Polytrichaceae (*Atrichum*, *Bartramiopsis**, *Meiotrichum*, *Oligotrichum**, *Pogonatum*, *Polytrichastrum*, *Polytrichum*)

Class Bryopsida

Subclass Funariidae

Order Timmiales

Family Timmiaceae (*Timmia*)

Order Encalyptales

Family Encalyptaceae (*Encalypta*)

Order Funariales

Family Funariaceae (*Aphanorrhagma**, *Entosthodon*, *Funaria*, *Physcomitrella*, *Physcomitrium*, *Pyramidula*)

Family Disceliaceae (*Discelium*)

Family Gigaspermaceae (*Lorentziella*)

Subclass Dicranidae

Order Grimmiiales

Family Grimmiaceae (*Coscinodon*, *Grimmia*, *Jaffueliobryum*, *Racomitrium*, *Schistidium*)Family Ptychomitriaceae (*Campylostelium**, *Ptychomitrium*)Family Scouleriaceae (*Scouleria*)

Order Archidiales

Family Archidiaceae (*Archidium*)

Order Seligeriales

Family Seligeriaceae (*Blindia*, *Brachydontium**, *Seligeria**)

Order Dicranales

Family Bryoxiphiaceae (*Bryoxiphium**)Family Fissidentaceae (*Fissidens*)Family Dicranaceae (*Arctoa*, *Atractyllocarpus*, *Campylopodiella*, *Campylopus*, *Dichodontium*, *Dicranella*, *Dicranodontium**, *Dicranum*, *Kiaeria*, *Orthodicranum*, *Paraleucobryum**)Family Bruchiaceae (*Bruchia*, *Trematodon*)Family Ditrichaceae (*Ceratodon*, *Distichium*, *Ditrichum*, *Pleuridium*, *Trichodon*)Family Rhabdoweisiaceae (*Amphidium*, *Cynodontium*, *Dichodontium*, *Dicranoweisia*, *Oncophorus*)Family Schistostegaceae (*Schistostega**)

Order Pottiales

Family Pottiaceae (*Acaulon*, *Aloina*, *Anoetangium**, *Barbula*, *Bryoerythrophyllum*, *Crossidium*, *Crumia*, *Didymodon*, *Eucladium*, *Gymnostomum*, *Henmediella*, *Hymenostylium*, *Leptophascum*, *Microbryum*, *Molendia*, *Oxystegus*, *Phascum*, *Plaubelia**, *Pseudocrossidium*, *Pterygoneurum*, *Scopelophila*, *Stegonia*, *Syntrichia*, *Timmia*, *Tortella*, *Tortula*, *Trichostomum*, *Triquetrella*, *Weissia*)Family Ephemeraceae (*Ephemerum*)

Subclass Bryidae

Superorder Bryanae

Order Splachnales

Family Splachnaceae (*Splachnum**, *Tayloria**, *Tetraplodon**)Family Meesiaceae (*Leptobryum*, *Meesia*)

Order Orthotrichales

Family Orthotrichaceae (*Orthotrichum*, *Ulota*, *Zygodon*)

Order Hedwigiales

Family Hedwigiaceae (*Braunia**, *Hedwigia*, *Pseudobraunia*)

Order Bryales

Family Aulacomniaceae (*Aulacomnium*)Family Bartramiaceae (*Anacolia*, *Bartramia*, *Conostomum*, *Philonotis*, *Plagiopus**)Family Orthodontiaceae (*Orthodontium*)Family Bryaceae (*Anomobryum*, *Brachymenium**, *Bryum*, *Plagiobryum**)Family Mniaceae (*Epipterygium*, *Leucolepis*, *Mnium*, *Plagiomnium*, *Pohlia*, *Rhizomnium*, *Roellia*)Family Mielichhoferiaceae (*Mielichhoferia*, *Schizymenium*)

Superorder Hypnanae

Order Hookeriales

Suborder Hookeriinae

Family Hookeriaceae (*Hookeria*)

Order Hypnales

Family Amblystegiaceae (*Amblystegium*, *Hygroamblystegium*, *Leptodictyum*, *Limbella**)Family Cratoneuraceae (*Cratoneuron*)Family Helodiaceae (*Helodium*, *Palustriella*)Family Hylocomiaceae (*Hylocomium*, *Pleurozium**, *Rhytidadelphus*, *Rhytidiopsis*)Family Rhytidiaceae (*Rhytidium**)Family Leskeaceae (*Claopodium*, *Leptopterygynandrum*, *Lescuraea*, *Leskea*, *Pseudoleskeella*)Family Pterigynandraceae (*Heterocladium*, *Iwatsukiella**, *Myurella*, *Pterigynandrum*)Family Thuidiaceae (*Thuidium**)Family Campyliaceae (*Calliargon*, *Campylium*, *Conardia*, *Drepanocladus*, *Hamatocaulis*, *Hygrohypnum*, *Pseudo-calliargon*, *Sanionia*, *Straminergon*, *Tomentypnum**, *Warnstorfia*)Family Brachytheciaceae (*Bestia*, *Brachythecium*, *Cirriphyllum**, *Eurhynchium*, *Homalothecium*, *Isothecium*, *Kindbergia*, *Platyhypnidium*, *Pseudoscleropodium*, *Scleropodium*, *Steerecleus*, *Trachybryum*)Family Fabroniaceae (*Fabronia*)Family Meteoraceae (*Meteorium**)Family Plagiotheciaceae (*Plagiothecium*)Family Fontinalaceae (*Dichelyma*, *Fontinalis*)Family Climaciaceae (*Climacium**)Family Hypnaceae (*Breidleria**, *Buckiella*, *Calliargonella*, *Herzogiella*, *Homomallium*, *Hypnum*, *Isopterygiopsis*, *Isopterygium*, *Orthothecium**, *Platydictya*, *Pseudotaxiphyllum*, *Ptilium** *Tripterocladium*, *Vesicularia*)Family Sematophyllaceae (*Sematophyllum*)Family Cryphaeaceae (*Dendroalsia*)Family Leucodontaceae (*Antitrichia*, *Pterogonium*)

Family Neckeraceae (*Bryolawtonia*, *Homalia**, *Metaneckera*, *Neckera*, *Porotrichum*, *Thamnobryum*)
 Family Leptodontaceae (*Alsia*)

APPENDIX II.

MOSSES OF THE STATES INCLUDED IN THIS WORK

Mosses known from California

Acaulon rufescens A. Jaeger
Acaulon triquetrum (Spruce) C. Müller Hal.
Aloina ambigua (Bruch & W. P. Schimper) Limpricht
Aloina bifrons (De Notaris) Delgadillo
Aloina rigida (Hedwig) Limpricht
Alsia californica (W. J. Hooker & Arnott) Sullivant
Amblystegium juratzkanum W. P. Schimper
Amblystegium serpens (Hedwig) Bruch & W. P. Schimper
Amblystegium varium (Hedwig) Lindberg
Amphidium californicum (Hampe ex C. Müller Hal.) Brotherus
Amphidium lapponicum (Hedwig) W. P. Schimper
Amphidium mougeotii (Bruch & W. P. Schimper) W. P. Schimper
Anacolia baueri Hampe
Anacolia laevisphaera (Taylor) Flowers in Grout
Anacolia menziesii (Turner) Paris
Andreaea alpestris (Thedenius) W. P. Schimper
Andreaea blyttii W. P. Schimper
Andreaea heinemannii Hampe & C. Müller Hal.
Andreaea nivalis W. J. Hooker
Andreaea rothii Weber & D. Mohr
Andreaea rupestris Hedwig
Andreaea schofieldiana B. M. Murray
Anomobryum julaceum (Schrader ex P. G. Gärtner, B. Meyer & Scherbius) W. P. Schimper
Antitrichia californica Sullivant in Lesquereux
Antitrichia gigantea (Renauld & Cardot) Kindberg
Archidium alternifolium (Dickson ex Hedwig) Mitten
Arctoa fulvella (Dickson) Bruch & W. P. Schimper
Atractyllocarpus flagellaceus (C. Müller Hal.) R. S. Williams
Atrichum selwynii Austin
Atrichum undulatum (Hedwig) Palisot de Beauvois
Aulacomnium androgynum (Hedwig) Schwägrichen
Aulacomnium palustre (Hedwig) Schwägrichen
Barbula convoluta Hedwig
Barbula ehrenbergii (Lorentz) Fleischer
Barbula eustegia Cardot & Thériot
Barbula unguiculata Hedwig
Bartramia ithyphylla Bridel
Bartramia pomiformis Hedwig
Bartramia stricta Bridel
Bestia longipes (Sullivant & Lesquereux) Brotherus
Blindia acuta (Hedwig) Bruch & W. P. Schimper
Brachythecium albicans (Hedwig) Bruch & W. P. Schimper
Brachythecium asperrimum (C. Müller Hal.) Sullivant
Brachythecium bolanderi (Lesquereux) A. Jaeger
Brachythecium calcareum Kindberg
Brachythecium collinum (Schleicher ex C. Müller Hal.) Bruch & W. P. Schimper
Brachythecium erythrorrhizon Bruch & W. P. Schimper
Brachythecium fendleri (Sullivant) A. Jaeger
Brachythecium frigidum (C. Müller Hal.) Bescherelle
Brachythecium holzingeri (Grout) Grout
Brachythecium hylotapetum N. Higinbotham & B. Higinbotham
Brachythecium leibergii Grout
Brachythecium nelsonii Grout
Brachythecium oedipodium (Mitten) A. Jaeger
Brachythecium plumosum (Hedwig) Bruch & W. P. Schimper
Brachythecium populeum (Hedwig) Bruch & W. P. Schimper
Brachythecium reflexum (Starke in Weber & D. Mohr) Bruch & W. P. Schimper
Brachythecium rivulare Bruch & W. P. Schimper
Brachythecium rutabulum (Hedwig) Bruch & W. P. Schimper

Brachythecium salebrosum (Weber & D. Mohr) Bruch & W. P. Schimper
Brachythecium starkei (Bridel) Bruch & W. P. Schimper
Brachythecium velutinum (Hedwig) Bruch & W. P. Schimper
Brachythecium venustum De Notaris
Bruchia bolanderi Lesquereux
Bruchia flexuosa (Schwägrichen) C. Müller Hal.
Bryoerythrophyllum columbianum (F. J. Hermann & E. Lawton) Zander
Bryoerythrophyllum recurvirostrum (Hedwig) Chen
Bryolawtonia vancouveriensis (Kindberg) Norris & Enroth
Bryum algovicum Sendtner *ex* C. Müller Hal.
Bryum alpinum Hudson *ex* Withering
Bryum amblyodon C. Müller Hal.
Bryum argenteum Hedwig
Bryum badium (Bridel) W. P. Schimper
Bryum barnesii Wood *in* W. P. Schimper
Bryum bicolor Dickson
Bryum binum (Schreber) Turner
Bryum blindii Bruch & W. P. Schimper
Bryum caespiticium Hedwig
Bryum calobryoides Spence
Bryum canariense Bridel
Bryum capillare Hedwig
Bryum cyclophyllum (Schwägrichen) Bruch & W. P. Schimper
Bryum elegans Nees *in* Bridel
Bryum erythroloma (Kindberg) Syed
Bryum flaccidum Bridel
Bryum gemmascens Kindberg
Bryum gemmiferum R. Wilczek & Demaret
Bryum gemmilucens R. Wilczek & Demaret
Bryum gemmiparum De Notaris
Bryum laevifilum Syed
Bryum lanatum (Palisot de Beauvois) Bridel
Bryum lisae De Notaris
Bryum meesioides Kindberg *in* Macoun
Bryum microerythrocarpum C. Müller Hal. & Kindberg
Bryum miniatum Lesquereux
Bryum muehlenbeckii Bruch & W. P. Schimper
Bryum pallens Swartz
Bryum pallescens Schleicher *ex* Schwägrichen
Bryum pseudotriquetrum (Hedwig) Gaertner, B. Meyer & Scherbius
Bryum pyriferum Crundwell & H. Whitehouse
Bryum radiculosum Bridel
Bryum rubens Mitten
Bryum subapiculatum Hampe
Bryum tenuisetum Limpricht
Bryum torquescens Bruch
Bryum turbinatum (Hedwig) Turner
Bryum uliginosum (Bridel) Bruch & W. P. Schimper
Bryum violaceum Crundwell & Nyholm
Bryum weigeliai Sprengel
Buckiella undulata (Hedwig) Ireland
Buxbaumia aphylla Hedwig
Buxbaumia piperi Best
Buxbaumia viridis (A. P. de Candolle) Mougeot & Nestler
Calliergonella cuspidata (Hedwig) Loeske
Campylium chrysophyllum (Bridel) J. M. Lange
Campylium hispidulum (Bridel) Mitten
Campylium polygamum (W. P. Schimper) C. E. O. Jensen
Campylium stellatum (Hedwig) C. E. O. Jensen
Campylopodiella stenocarpa (Wilson *in* Seemann) P. Müller & Frahm
Campylopus introflexus (Hedwig) Bridel
Campylopus pyriformis (F. Schultz) Bridel
Campylopus schmidii (C. Müller Hal.) A. Jaeger
Campylopus subulatus W. P. Schimper *in* Rabenhorst
Ceratodon purpureus (Hedwig) Bridel
Ceratodon stenocarpus Bruch & W. P. Schimper
Claopodium bolanderi Best
Claopodium crispifolium (W. J. Hooker) Renaud & Cardot

- Cladopodium whippleanum* (Sullivant) Renauld & Cardot
Conardia compacta (C. Müller Hal.) H. Robinson
Conostomum tetragonum (Hedwig) Lindberg
Coscinodon calyptratus (Drummond) C. E. O. Jensen in Kindberg
Cratoneuron filicinum (Hedwig) Spruce
Crossidium aberrans Holzinger & E. B. Bartram
Crossidium crassinerve (De Notaris) Juratzka
Crossidium seriatum H. Crum & W. C. Steere
Crossidium squamiferum (Viviani) Juratzka
Crumia latifolia (Kindberg ex Macoun) W. B. Schofield
Cynodontium jenneri (W. P. Schimper in Howie) Stirton
Cynodontium tenellum (Bruch & W. P. Schimper) Limpricht
Dacryophyllum falcifolium Ireland
Dendroalsia abietina (W. J. Hooker) E. Britton in Brotherus
Dichelyma uncinatum Mitten
Dichodontium flavescens (Dickson) Lindberg
Dichodontium olympicum Renauld & Cardot
Dichodontium pellucidum (Hedwig) W. P. Schimper
Dicranella crispa (Hedwig) W. P. Schimper
Dicranella heteromalla (Hedwig) W. P. Schimper
Dicranella hilariana (Montagne) Mitten
Dicranella howei Renauld & Cardot
Dicranella pacifica W. B. Schofield
Dicranella palustris (Dickson) Crundwell ex Warburg
Dicranella rufescens (Withering) W. P. Schimper
Dicranella schreberiana (Hedwig) Hilferty
Dicranella subulata (Hedwig) W. P. Schimper
Dicranoweisia cirrata (Hedwig) Lindberg in Milde
Dicranoweisia contermina Renauld & Cardot
Dicranum fuscescens Turner
Dicranum howellii Renauld & Cardot
Dicranum scoparium Hedwig
Dicranum sulcatum Kindberg in Macoun
Dicranum undulatum Schrader ex Bridel
Didymodon australasiae (W. J. Hooker & Greville) Zander
Didymodon brachyphyllus (Sullivant in Whipple) Zander
Didymodon eckeliae Zander
Didymodon fallax (Hedwig) Zander
Didymodon ferrugineus (W. P. Schimper ex Bescherelle) M. O. Hill
Didymodon insulanus (De Notaris) M. O. Hill
Didymodon nicholsonii Culmann
Didymodon norrisii Zander
Didymodon occidentalis Zander
Didymodon revolutus (Cardot) R. S. Williams
Didymodon rigidulus Hedwig
Didymodon tophaceus (Bridel) Lisa
Didymodon umbrosus (C. Müller Hal.) Zander
Didymodon vinealis (Bridel) Zander
Discelium nudum (Dickson) Bridel
Distichium capillaceum (Hedwig) Bruch & W. P. Schimper
Distichium inclinatum (Hedwig) Bruch & W. P. Schimper
Ditrichum ambiguum Best
Ditrichum heteromallum (Hedwig) E. Britton
Ditrichum montanum Leiberg
Ditrichum pusillum (Hedwig) Hampe
Ditrichum schimperi (Lesquereux) Kuntze
Drepanocladus aduncus (Hedwig) Warnstorf
Drepanocladus capillifolius (Warnstorf) Warnstorf
Drepanocladus polycarpus (Blandow ex Voit) Warnstorf
Drepanocladus sordidus (C. Müller Hal.) Hedenäs in W. R. Buck
Encalypta ciliata Hedwig
Encalypta intermedia Juratzka
Encalypta procera Bruch
Encalypta rhaptocharpa Schwägrichen
Encalypta vulgaris Hedwig
Entosthodon attenuatus (Dickson) Bryhn
Entosthodon bolanderi Lesquereux
Entosthodon californicus (Sullivant & Lesquereux) H. Crum & L. E. Anderson

Entosthodon drummondii Sullivant in Sullivant & Lesquereux
Entosthodon kochii H. Crum & L. E. Anderson
Entosthodon rubrissetus (E. B. Bartram) Grout
Entosthodon tucsoni (E. B. Bartram) Grout
Ephemerum serratum (Schreber ex Hedwig) Hampe
Epipterygium tozeri (Greville) Lindberg
Eucladium verticillatum (Hedwig in Bridel) Bruch & W. P. Schimper
Eurhynchium hians (Hedwig) Sande Lacoste
Eurhynchium pulchellum (Hedwig) Jennings
Eurhynchium striatum (Schreber ex Hedwig) W. P. Schimper
Fabronia ciliaris (Bridel) Bridel
Fabronia pusilla Raddi
Fissidens adianthoides Hedwig
Fissidens aphelotaxifolius Pursell
Fissidens bryoides Hedwig
Fissidens crispus Montagne
Fissidens curvatus Hornschuch
Fissidens dubius Palisot de Beauvois
Fissidens fontanus (Bachelot de la Pylaie) Steudel
Fissidens grandifrons Bridel
Fissidens minutulus Sullivant
Fissidens pauperculus M. A. Howe
Fissidens sublimbatus Grout
Fissidens taxifolius Hedwig
Fissidens taylorii C. Müller Hal.
Fissidens ventricosus Lesquereux
Fontinalis antipyretica Hedwig
Fontinalis chrysophylla Cardot
Fontinalis gigantea Sullivant
Fontinalis howellii Renauld & Cardot
Fontinalis hypnoides C. J. Hartman
Fontinalis mollis C. Müller Hal.
Fontinalis neomexicana Sullivant & Lesquereux
Funaria calvescens Schwägrichen
Funaria hygrometrica Hedwig
Funaria microstoma Bruch ex W. P. Schimper
Funaria muhlenbergii Turner
Grimmia alpestris (Weber & D. Mohr) Schleicher
Grimmia anodon Bruch & W. P. Schimper
Grimmia anomala Hampe in W. P. Schimper
Grimmia arcuatifolia Kindberg
Grimmia caespiticia (Bridel) Juratzka
Grimmia hamulosa Lesquereux
Grimmia laevigata (Bridel) Bridel
Grimmia leibergii Paris
Grimmia lesherae H. C. Greven
Grimmia lisae De Notaris
Grimmia longirostris W. J. Hooker
Grimmia mariniana Sayre
Grimmia mollis Bruch & W. P. Schimper
Grimmia montana Bruch & W. P. Schimper
Grimmia moxleyi R. S. Williams in Holzinger
Grimmia nevadensis H. C. Greven
Grimmia orbicularis Bruch in Wilson
Grimmia ovalis (Hedwig) Lindberg
Grimmia plagiopodia Hedwig
Grimmia poecilostoma Cardot & Seville
Grimmia pulvinata (Hedwig) J. E. Smith
Grimmia ramondii (Lamarck & A. P. de Candolle) Margadant
Grimmia reflexidens C. Müller Hal.
Grimmia serrana Muñoz, Shevock & Toren
Grimmia shastae H. C. Greven
Grimmia tergestina Tommasini ex Bruch & W. P. Schimper
Grimmia torquata Drummond
Grimmia trichophylla Greville
Grimmia ungeri Juratzka in Unger & Kotschy
Gymnostomum calcareum Nees & Hornschuch
Hamatocaulis vernicosus (Mitten) Hedenäs

- Hedwigia detonsa* (Howe) W. R. Buck & Norris
Hedwigia stellata Hedenäs
Helodium blandowii (Weber & D. Mohr) Warnstorf
Hennediella heimii (Hedwig) Zander
Hennediella stanfordensis (W. C. Steere) Blockeel
Herzogiella seligeri (Bridel) Iwatsuki
Herzogiella striatella (Bridel) Iwatsuki
Heterocladium dimorphum (Bridel) W. P. Schimper in Bruch & W. P. Schimper
Heterocladium macounii Best
Homalothecium aeneum (Mitten) E. Lawton
Homalothecium arenarium (Lesquereux) E. Lawton
Homalothecium fulgescens (Mitten ex C. Müller Hal.) E. Lawton
Homalothecium nevadense (Lesquereux) Renauld & Cardot
Homalothecium nuttallii (Wilson) A. Jaeger
Homalothecium pinnatifidum (Sullivant & Lesquereux) E. Lawton
Homomallium mexicanum Cardot
Hookeria lucens (Hedwig) J. E. Smith
Hygroamblystegium tenax (Hedwig) Jennings
Hygrohypnum alpinum (Lindberg) Loeske
Hygrohypnum bestii (Renauld & Bryhn) Brotherus
Hygrohypnum cochlearifolium (Venturi in De Notaris) Brotherus
Hygrohypnum duriusculum (De Notaris) Jamieson
Hygrohypnum luridum (Hedwig) Jennings
Hygrohypnum molle (Hedwig) Loeske
Hygrohypnum ochraceum (Turner ex Wilson) Loeske
Hygrohypnum smithii (Swartz in Liljeblad) Brotherus
Hygrohypnum styriacum (Limpricht) Brotherus
Hylocomium splendens (Hedwig) Bruch & W. P. Schimper
Hymenostylium recurvirostre (Hedwig) Dixon
Hypnum circinale W. J. Hooker
Hypnum dieckii Renauld & Cardot
Hypnum lindbergii Mitten
Hypnum revolutum (Mitten) Lindberg
Hypnum subimponens Lesquereux
Hypnum vaucheri Lesquereux
Isopterygiopsis pulchella (Hedwig) Iwatsuki
Isopterygium tenerum (Swartz) Mitten
Isothecium cardotii Kindberg
Isothecium cristatum (Hampe) H. Robinson
Isothecium myosuroides Bridel
Isothecium obtusatum Kindberg
Isothecium spiculiferum (Mitten) Renauld & Cardot
Isothecium stoloniferum Bridel
Jaffuelobryum raui (Austin) Thériot
Jaffuelobryum wrightii Sullivant in Sullivant & Lesquereux
Kiaeria blyttii (Bruch & W. P. Schimper) Brotherus
Kiaeria falcata (Hedwig) I. Hagen
Kiaeria starkei (Weber & D. Mohr) I. Hagen
Kindbergia oregana (Sullivant) Ochyra
Kindbergia praelonga (Hedwig) Ochyra
Leptobryum pyriforme (Hedwig) Wilson
Leptodictyum humile (Palisot de Beauvois) Ochyra
Leptodictyum riparium (Hedwig) Warnstorf
Leptophascum leptophyllum (C. Müller Hal.) J. Guerra & M. J. Cano
Leptopterigynandrum austro-alpinum C. Müller Hal.
Lescuraea atricha (Kindberg in Macoun & Kindberg) E. Lawton
Lescuraea incurvata (Hedwig) E. Lawton
Lescuraea pallida (Best) Norris & Shevock
Lescuraea patens (Lindberg) Arnott & C. E. O. Jensen
Lescuraea radicata (Mitten) Mönkemeyer
Lescuraea saviana (De Notaris) E. Lawton
Lescuraea stenophylla (Renauld & Cardot) Lindberg
Leskea polycarpa Ehrhart ex Hedwig
Leucolepis acanthoneura (Schwägrichen) Lindberg
Lorentziella imbricata (Mitten) Brotherus
Meesia longiseta Hedwig
Meesia triquetra (H. Richter) Ångström
Meesia uliginosa Hedwig

Meiotrichum lyallii (Mitten) G. L. S. Merrill
Metaneckera menziesii (Drummond) W. C. Steere
Microbryum davallianum (J. E. Smith in Drake) Zander
Microbryum starckeanum (Hedwig) Zander
Mielichhoferia elongata (Hoppe & Hornschuch in W. J. Hooker) Nees & Hornschuch
Mielichhoferia tehamensis Showers
Mnium arizonicum Amann
Mnium blyttii Bruch & W. P. Schimper
Mnium marginatum (Dickson ex Withering) Palisot de Beauvois
Mnium spinulosum Bruch & W. P. Schimper
Mnium thomsonii W. P. Schimper
Molendoo sendtneriana (Bruch & W. P. Schimper) Limpricht
Myurella julacea (Schwägrichen in Schultes) Bruch & W. P. Schimper
Neckera douglasii W. J. Hooker
Oncophorus virens (Hedwig) Bridel
Oncophorus wahlenbergii Bridel
Orthodicranum tauricum (Sapehin) Smirnova
Orthodontium gracile (Wilson in J. E. Smith) Schwägrichen ex Bruch & W. P. Schimper
Orthodontium pellucens (W. J. Hooker) Bruch & W. P. Schimper in C. Müller Hal.
Orthotrichum affine Schrader ex Bridel
Orthotrichum alpestre Hornschuch ex Bruch & W. P. Schimper
Orthotrichum bolanderi Sullivant
Orthotrichum consimile Mitten
Orthotrichum cupulatum G. F. Hoffman ex Bridel
Orthotrichum diaphanum Schrader ex Bridel
Orthotrichum euryphyllum Venturi in Röhl
Orthotrichum flowersii Vitt
Orthotrichum hallii Sullivant & Lesquereux in Sullivant
Orthotrichum holzingeri Renauld & Cardot in Holzinger
Orthotrichum laevigatum J. E. Zetterstedt
Orthotrichum lyellii W. J. Hooker & Taylor
Orthotrichum macounii Austin
Orthotrichum obtusifolium Bridel
Orthotrichum pallens Bruch ex Bridel
Orthotrichum papillosum Hampe
Orthotrichum pellucidum Lindberg
Orthotrichum praemorsum Venturi
Orthotrichum pulchellum Brunton in J. E. Smith
Orthotrichum pumilum Swartz
Orthotrichum pylaisii Bridel
Orthotrichum rivulare Turner
Orthotrichum rupestre Schleicher ex Schwägrichen
Orthotrichum shevockii Lewinsky-Haapasaari & Norris
Orthotrichum speciosum Nees in J. W. Sturm
Orthotrichum spjutii Norris & Vitt
Orthotrichum striatum Hedwig
Orthotrichum tenellum Bruch ex Bridel
Orthotrichum texanum Sullivant & Lesquereux
Orthotrichum underwoodii F. Lara, Gariletti & Mazimpaka
Oxystegus tenuirostris (W. J. Hooker & Taylor) A. J. E. Smith
Palustriella commutata (Bridel) Ochyra
Phascum cuspidatum Hedwig
Philonotis americana (Dismier) Dismier
Philonotis caespitosa Juratzka
Philonotis calcarea (Bruch & W. P. Schimper) W. P. Schimper
Philonotis capillaris Lindberg
Philonotis fontana (Hedwig) Bridel
Philonotis marchica (Hedwig) Bridel
Philonotis muehlenbergii (Schwägrichen) Bridel
Philonotis tomentella Molendo in Lorentz
Philonotis yezoana Bescherelle & Cardot
Physcomitrella patens (Hedwig) Bruch & W. P. Schimper
Physcomitrella readeri (C. Müller Hal.) Stone & G. A. M. Scott
Physcomitrium californicum E. Britton
Physcomitrium collenchymatum Gier
Physcomitrium hookeri Hampe
Physcomitrium pyriforme (Hedwig) Hampe
Plagiomnium cuspidatum (Hedwig) T. Koponen

- Plagiomnium ellipticum* (Bridel) T. Koponen
Plagiomnium insigne (Mitten) T. Koponen
Plagiomnium medium (Bruch & W. P. Schimper) T. Koponen
Plagiomnium rostratum (Schrader) T. Koponen
Plagiomnium venustum (Mitten) T. Koponen
Plagiothecium cavifolium (Bridel) Iwatsuki
Plagiothecium denticulatum (Hedwig) Bruch & W. P. Schimper
Plagiothecium laetum Bruch & W. P. Schimper
Plagiothecium piliferum (Swartz ex C. J. Hartman) Bruch & W. P. Schimper
Platydictya jungermannioides (Bridel) H. Crum
Platyhypnidium riparioides (Hedwig) Dixon
Pleuridium acuminatum Lindberg
Pleuridium subulatum (Hedwig) Rabenhorst
Pogonatum contortum (Menzies ex Bridel) Lesquereux
Pohlia andalusica (Höhnelt) Brotherus
Pohlia annotina (Hedwig) Lindberg
Pohlia bolanderi (Lesquereux) Brotherus
Pohlia camptotrachela (Renauld & Cardot) Brotherus
Pohlia cardotii (Renauld in Renauld & Cardot) Brotherus
Pohlia cruda (Hedwig) Lindberg
Pohlia drummondii (C. Müller Hal.) Andrews in Grout
Pohlia elongata Hedwig
Pohlia filum (W. P. Schimper) Mårtensson
Pohlia lescuriana (Sullivant) Ochi
Pohlia longibracteata Brotherus in Röhl
Pohlia ludwigii (Sprengel ex Schwägrichen) Brotherus
Pohlia nutans (Hedwig) Lindberg
Pohlia obtusifolia (Villars ex Bridel) L. Koch
Pohlia pacifica A. J. Shaw
Pohlia prolifera (Kindberg) Brotherus
Pohlia tundrae A. J. Shaw
Pohlia wahlenbergii (Weber & D. Mohr) Andrews in Grout
Polytrichastrum alpinum (Hedwig) G. L. Smith
Polytrichum commune Hedwig
Polytrichum formosum Hedwig
Polytrichum juniperinum Hedwig
Polytrichum longisetum Swartz ex Bridel
Polytrichum piliferum Hedwig
Polytrichum sexangulare Flörke ex Bridel
Polytrichum strictum Bridel
Porotrichum bigelovii (Sullivant) Kindberg
Pseudobraunia californica (Lesquereux) Brotherus
Pseudo-calliaron angustifolium Hedenäs
Pseudo-calliaron trifarium (Weber & D. Mohr) Loeske
Pseudocrossidium crinitum (Schultz) Zander
Pseudocrossidium obtusulum (Lindberg) H. Crum & L. E. Anderson
Pseudoleskeella serpentinensis P. Wilson & Norris
Pseudoleskeella tectorum (Funck ex Bridel) Kindberg ex Brotherus
Pseudoscleropodium purum (Hedwig) Fleischer in Brotherus
Pseudotaxiphyllum elegans (Bridel) Iwatsuki
Pterigynandrum filiforme Hedwig
Pterogonium gracile (Hedwig) J. E. Smith
Pterygoneurum californicum H. Crum
Pterygoneurum lamellatum (Lindberg) Juratzka
Pterygoneurum ovatum (Hedwig) Dixon
Pterygoneurum subsessile (Bridel) Juratzka
Ptychomitrium gardneri Lesquereux
Pyramidula tetragona (Bridel) Bridel
Racomitrium aciculare (Hedwig) Bridel
Racomitrium affine (Schleicher ex Weber & D. Mohr) Lindberg
Racomitrium depressum Lesquereux
Racomitrium elongatum Ehrhart ex Frisvoll
Racomitrium ericoides (Hedwig) Bridel
Racomitrium fasciculare (Hedwig) Bridel
Racomitrium heterostichum (Hedwig) Bridel
Racomitrium lanuginosum (Hedwig) Bridel
Racomitrium lawtonae Ireland
Racomitrium macounii Kindberg

Racomitrium microcarpon (Hedwig) Bridel
Racomitrium molle Cardot
Racomitrium norrisii Bednarek-Ochyra & Ochyra
Racomitrium obesum Frisvoll
Racomitrium occidentale (Renauld & Cardot) Renauld & Cardot
Racomitrium pacificum Ireland & Spence
Racomitrium sudeticum (Funck) Bruch & W. P. Schimper
Racomitrium varium (Mitten) A. Jaeger
Rhizomnium glabrescens (Kindberg) T. Koponen
Rhizomnium magnifolium (Horikawa) T. Koponen
Rhizomnium pseudopunctatum (Bruch & W. P. Schimper) T. Koponen
Rhizomnium punctatum (Hedwig) T. Koponen
Rhytidiadelphus loreus (Hedwig) Warnstorf
Rhytidiadelphus squarrosus (Hedwig) Warnstorf
Rhytidiadelphus triquetrus (Hedwig) Warnstorf
Rhytidiopsis robusta (W. J. Hooker) Brotherus
Roellia roellii (Brotherus ex Röhl) Andrews ex H. Crum
Sanionia uncinata (Hedwig) Loeske
Schistidium agassizii Sullivant & Lesquereux in Sullivant
Schistidium atrichum (C. Müller Hal. & Kindberg) W. A. Weber
Schistidium cinclidontium (C. Müller Hal. in Röhl) B. Bremer
Schistidium confertum (Funck) Bruch & W. P. Schimper
Schistidium dupretii (Thériot) W. A. Weber
Schistidium flaccidum (De Notaris) Ochyra
Schistidium maritimum (Turner ex Scott) Bruch & W. P. Schimper
Schistidium occidentale (E. Lawton) Churchill in Funk & D. R. Brooks
Schistidium platyphyllum (Mitten) Persson in Persson & Gjaerev
Schistidium rivulare (Bridel) Podpera
Schistidium tenerum (J. E. Zetterstedt) Nyholm
Schizymerium shevockii A. J. Shaw
Scleropodium californicum (Lesquereux) Kindberg
Scleropodium cespitosum (Wilson ex C. Müller Hal.) L. Koch
Scleropodium colpophyllum (Sullivant) Grout
Scleropodium julaceum E. Lawton
Scleropodium obtusifolium (Mitten) Kindberg in Macoun
Scleropodium touretii (Bridel) L. Koch
Scopelophila cataractae (Mitten) Brotherus
Scouleria aquatica W. J. Hooker in Drummond
Scouleria marginata E. Britton
Sematophyllum adnatum (Michaux) E. Britton
Sphagnum bartlettianum Warnstorf
Sphagnum capillifolium (Ehrhart) Hedwig
Sphagnum compactum Lamarck & A. P. de Candolle
Sphagnum contortum Schultz
Sphagnum fimbriatum Wilson in W. J. Hooker
Sphagnum fuscum (W. P. Schimper) Klinggräff
Sphagnum girgensohnii Russow
Sphagnum henryense Warnstorf
Sphagnum inundatum Russow
Sphagnum lescurii Sullivant in A. Gray
Sphagnum magellanicum Bridel
Sphagnum mendocinum Sullivant
Sphagnum palustre Linnaeus
Sphagnum papillosum Lindberg
Sphagnum platyphyllum (Lindberg) Warnstorf
Sphagnum quinquefarium (Lindberg in Braithwaite) Warnstorf
Sphagnum russowii Warnstorf
Sphagnum squarrosum Crome in Hoppe
Sphagnum strictum Sullivant
Sphagnum subnitens Russow & Warnstorf
Sphagnum subsecundum Nees in Sturm
Sphagnum teres (W. P. Schimper) Ångström in C. J. Hartman
Sphagnum warnstorffii Russow
Steerecleus serrulatus (Hedwig) H. Robinson
Stegonia hyalinotricha (Cardot & Thériot) Zander
Stegonia latifolia (Schwägrichen in Schultes) Venturi ex Brotherus
Stegonia pilifera (Bridel) H. Crum & L. E. Anderson
Straminergon stramineum (Dickson ex Bridel) Hedenäs

Syntrichia amplexa (Lesquereux) Zander
Syntrichia bartramii (W. C. Steere in Grout) Zander
Syntrichia bolanderi (Lesquereux & T. P. James) Zander
Syntrichia caninervis Mitten
Syntrichia laevipila Bridel
Syntrichia latifolia (Bruch ex C. J. Hartman) Hübener
Syntrichia norvegica Weber
Syntrichia obtusissima (C. Müller Hal.) Zander
Syntrichia pagorum (Milde) Amann
Syntrichia papillosa (Wilson in Spruce) Juratzka
Syntrichia papillosissima (Coppey) Loeske
Syntrichia princeps (De Notaris) Mitten
Syntrichia ruralis (Hedwig) Weber & D. Mohr
Tetraphis pellucida Hedwig
Thamnobryum neckeroides (W. J. Hooker) E. Lawton
Timmia austriaca Hedwig
Timmia bavarica Hessler
Timmia anomala (Bruch & W. P. Schimper) Limpricht
Timmia crassinervis (Hampe) L. Koch
Tortella alpicola Dixon
Tortella fragilis (W. J. Hooker & Wilson in Drummond) Limpricht
Tortella tortuosa (Hedwig) Limpricht
Tortula atrovirens (J. E. Smith) Lindberg
Tortula brevipes (Lesquereux) Brotherus
Tortula californica E. B. Bartram
Tortula euryphylla Zander
Tortula guepinii (Bruch & W. P. Schimper) Brotherus
Tortula inermis Bridel
Tortula leucostoma (R. Brown) W. J. Hooker & Greville
Tortula mucronifolia Schwägrichen
Tortula muralis Hedwig
Tortula obtusifolia (Schwägrichen) Mathieu
Tortula plinthobia (Sullivant & Lesquereux in A. Gray) Brotherus
Tortula protobryoides Zander
Tortula subulata Hedwig
Tortula systylia (W. P. Schimper) Lindberg
Tortula truncata (Hedwig) Mitten in Godman
Trachybryum megaptilum (Sullivant) W. B. Schofield
Trematodon boasii W. B. Schofield
Trichodon cylindricus (Hedwig) W. P. Schimper
Trichostomum brachydontium Bruch in F. A. Müller
Trichostomum crispulum Bruch in F. A. Müller
Trichostomum sweetii (E. B. Bartram) Stark
Tripterocladium leucocladulum (C. Müller Hal.) A. Jaeger
Triquetrella californica (Lesquereux) Grout
Ulota megalospora Venturi in Röhl
Ulota obtusiuscula C. Müller Hal. & Kindberg in Macoun
Ulota phyllantha Bridel
Vesicularia vesicularis (Schwägrichen) Brotherus
Warnstorfia exannulata (Bruch & W. P. Schimper) Loeske
Warnstorfia fluitans (Hedwig) Loeske
Weissia andersoniana Zander
Weissia andrewsii E. B. Bartram
Weissia condensa (Voit in J. W. Sturm) Lindberg
Weissia controversa Hedwig
Weissia inoperculata (H. Crum) H. Crum, W. C. Steere & L. E. Anderson
Weissia ligulaefolia (E. B. Bartram) Grout
Zygodon menziesii (Schwägrichen) Arnott
Zygodon rupestris W. P. Schimper ex Lorentz

Mosses known from Oregon but not yet known from California

Aphanorrhagma serratum (W. J. Hooker & Wilson) Sullivant in A. Gray
Arctoa hyperborea (Withering) Bruch & W. P. Schimper
Brachydontium olympicum (E. Britton) McIntosh & Spence
Breidleria pratensis (Koch) Loeske
Calliergon cordifolium (Hedwig) Kindberg
Calliergon giganteum (W. P. Schimper) Kindberg

Climacium dendroides (Hedwig) Weber & D. Mohr
Dichelyma falcatum (Hedwig) Myrin
Dicranodontium denudatum (Bridel) E. Britton in R. S. Williams
Dicranoweisia roellii Kindberg in Röll
Dicranum fragilifolium Lindberg
Dicranum pallidisetum Ireland
Dicranum polysetum Swartz
Dicranum spadiceum J. E. Zetterstedt
Ditrichum flexicaule (Schwägrichen) Hampe
Encalypta brevicollis (Bruch & W. P. Schimper) Ångström
Encalypta brevipes Schljakov
Entosthodon fascicularis (Hedwig) C. Müller Hal.
Fissidens asplenioides Hedwig
Fissidens osmundioides Hedwig
Grimmia elatior Bruch ex Balsamo & De Notaris
Hedwigia ciliata (Hedwig) Palisot de Beauvois
Heterocladium procurrens (Mitten) A. Jaeger
Homalia trichomanoides (Hedwig) Bruch & W. P. Schimper
Hookeria acutifolia Hooker & Greville
Hypnum fertile Sendtner
Iwatsukiella leucotricha (Mitten) W. R. Buck & H. Crum
Lescuraea baileyi (Best & Grout in Grout) E. Lawton
Limbella fryei (R. S. Williams) Ochyra
Mnium ambiguum H. Müller
Oligotrichum aligerum Mitten
Oligotrichum hercynicum (Hedwig) Lamarck & A. P. de Candolle
Orthotrichum anomalum Hedwig
Physcomitrium immersum Sullivant
Plagiobryum zierii (Hedwig) Lindberg
Plagiomnium drummondii (Bruch & W. P. Schimper) T. Koponen
Plagiopus oederianus (Swartz) H. Crum & L. E. Anderson
Pleurozium schreberi (Bridel) Mitten
Pogonatum dentatum (Bridel) Bridel
Pogonatum urnigerum (Hedwig) Palisot de Beauvois
Pohlia sphagnicola (Bruch & W. P. Schimper) Lindberg & Arnell
Ptilium crista-castrensis (Hedwig) De Notaris
Racomitrium brevipes Kindberg in Macoun
Rhizomnium nudum (E. Britton & R. S. Williams) T. Koponen
Rhytidiadelphus subpinnatus (Lindberg) T. Koponen
Rhytidium rugosum (Hedwig) Kindberg
Schistostega pennata (Hedwig) Weber & D. Mohr
Sphagnum angustifolium (C. E. O. Jensen ex Russow) C. E. O. Jensen in Tolf
Sphagnum fallax (Klinggräff) Klinggräff
Sphagnum rubellum Wilson
Sphagnum tenellum (Bridel) Bory
Splachnum ampullaceum Hedwig
Tayloria hornschurchii (Greville & Arnott) Brotherus
Tayloria serrata (Hedwig) Bruch & W. P. Schimper
Tetraphis geniculata Girgensohn ex Milde
Tetraplodon mnioides (Hedwig) Bruch & W. P. Schimper
Thuidium recognitum (Hedwig) Lindberg
Tomentypnum nitens (Hedwig) Loeske

Mosses known from Washington but not yet known from Oregon or California

Anoetangium aestivum (Hedwig) Mitten
Atrichum tenellum (Röhling) Bruch & W. P. Schimper
Bartramia halleriana Hedwig
Bartramiopsis lescurii (T. P. James) Kindberg
Brachydontium trichodes (Weber) Milde
Brachythecium laetum (Bridel) Bruch & W. P. Schimper
Bryoxiphium norvegicum (Bridel) Mitten
Bryum arcticum (R. Brown) Bruch & W. P. Schimper
Bryum knowltonii Barnes
Bryum schleicheri Schwägrichen
Campylium radicale (Palisot de Beauvois) Grout
Campylopus atrovirens De Notaris
Campylostelium saxicola (Weber & D. Mohr) Bruch & W. P. Schimper

Cirriphyllum cirrosum (Schwägrichen in Schultes) Grout
Coscinodon cribrosus (Hedwig) Spruce
Cynodontium strumulosum C. Müller & Kindberg in Macoun
Dicranella grevilleana (Bridel) W. P. Schimper
Dicranella varia (Hedwig) W. P. Schimper
Dicranum majus Turner
Dicranum rhabdocarpum Sullivan
Drepanocladus crassicosatus Janssens
Encalypta affinis R. A. Hedwig in Weber & D. Mohr
Gymnostomum aeruginosum Nees & Hornschuch
Hypnum callichroum Bridel
Hypnum cupressiforme Hedwig
Oedipodium griffithianum (Dickson) Schwägrichen
Oligotrichum parallelum (Mitten) Kindberg
Orthothecium chryseum (Schwägrichen in Schultes) W. P. Schimper in Bruch & W. P. Schimper
Palustriella falcata (Bridel) Hedenäs
Paraleucobryum enerve (Thedenius in C. J. Hartman) Loeske
Physomitrium pygmaeum T. P. James
Pohlia vexans (Limpricht) H. Lindberg
Pseudo-calliergon turgescens (T. Jensen) Loeske
Racomitrium pygmaeum Frisvoll
Racomitrium rysardii Bednarek-Ochyra
Rhizomnium gracile T. Koponen
Sarmentypnum sarmentosum (Wahlenberg) Tuomikoski & T. Koponen
Seligeria campylopoda Kindberg in Macoun
Seligeria donniana (Smith) C. Müller Hal.
Seligeria recurvata (Hedwig) Bruch & W. P. Schimper
Sphagnum centrale C. E. O. Jensen
Sphagnum imbricatum Hornschuch ex Russow
Sphagnum recurvum Palisot de Beauvois
Splachnum sphaericum Hedwig
Splachnum vasculosum Hedwig
Tayloria lingulata (Dickson) Lindberg
Tetodontium brownianum (Dickson) Schwägrichen
Tetodontium repandum (Funck in Sturm) Schwägrichen
Timmia megapolitana Hedwig

Mosses known from Nevada but not yet known from Washington, Oregon, or California

Didymodon nevadensis Zander in Zander, Stark & Marrs-Smith
Entosthodon planoconvexus (E. B. Bartram) Grout
Grimmia americana E. B. Bartram
Grimmia unicolor W. J. Hooker in Greville

Mosses known from Baja California Norte but not yet known from Nevada, Washington, Oregon, or California

Aloina roseae (R. S. Williams) Delgadillo
Archidium donnellii Austin
Barbula orizabensis C. Müller Hal.
Brachymenium exile (Dozy & Molkenboer) Bosch & Sande le Coste
Brachymenium spirifolium (C. Müller Hal.) A. Jaeger
Brachymenium systylium (C. Müller Hal.) A. Jaeger
Brachythecium occidentale (Hampe) A. Jaeger
Braunia secunda (W. J. Hooker) Bruch & W. P. Schimper
Campylopus pilifer Bridel
Didymodon tectorum (C. Müller Hal.) K. Saito
Grimmia pilifera Palisot de Beauvois
Meteorium nigrescens (Swartz ex Hedwig) Dozy & Molkenboer
Philonotis uncinata (Schwägrichen) Bridel
Plaubelia sprengelii (Schwägrichen) Zander
Ptychomitrium sinense (Mitten) A. Jaeger
Ptychomitrium serratum (C. Müller Hal.) Bruch & W. P. Schimper ex Bescherele
Weissia planifolia Dixon
Weissia sinaloensis E. B. Bartram

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Editor—DR. JOHN CALLAWAY
Dept. of Environmental Science
University of San Francisco
2130 Fulton Street
San Francisco, CA 94117-1080
callaway@usfca.edu

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CYOPTERUS BECKII, A RARE PROTOGYNOUS UMBELLIFER
(APIACEAE) OF CAPITOL REEF NATIONAL PARK, CENTRAL UTAH

VINCENT J. TEPEDINO¹ AND SUSANNA M. MESSINGER

USDA ARS Bee Biology and Systematics Laboratory, Department of Biology,
Utah State University, Logan, UT 84322-5310

ABSTRACT

Protogyny in an andromonoecious apioid, *Cymopterus beckii*, is described. This rare western endemic of Capitol Reef National Park, and a few other sites in Utah and Arizona, is unusual in producing only inflorescences with compound primary umbels; secondary and tertiary umbels are absent. Outer flowers of umbels produce significantly higher percentages of pistillate flowers than do inner flowers. On average, approximately 1.5 staminate flowers are produced for each pistillate flower. Within umbels, dichogamy is complete: female parts of pistillate flowers throughout the umbel mature first, followed by staminate. The small flowers are visited by a variety of flies, beetles, wasps and bees, few of which appear to carry pollen. Bees in the family Halictidae may be the most important pollinators, but additional studies are required to establish this.

Key Words: Apiaceae, *Cymopterus*, andromonoecy, protogyny, rare plant, pollinator.

Approximately 10 to 20% of angiosperms are monoecious, andromonoecious or gynodioecious (Bertin 1982). Andromonoecy, the presence of pistillate and staminate flowers on the same plant, is especially well represented in the Apiaceae (Umbelliferae) (Lovett Doust 1980; Webb 1981). Until recently (Schlessman and Barrie in press), flower development by andromonoecious umbellifers was considered to be primarily protandrous, i.e., anthers dehisce before the stigmas become receptive; the reverse condition, protogyny, was considered rare (Bell 1971; Webb 1981). However, many protogynous andromonoecious apioids are now being found, particularly in the Americas (Schlessman and Barrie in press), and the phenomenon has been reported for several apioid genera (*Lomatium*: Schlessman 1978, 1982; Kaye 1992; *Thaspium*, *Zizia*: Lindsey 1982; *Myrrhidendron*: Webb 1984; *Pseudocymopterus*: Schlessman and Graceffa 2002). Indeed, the discovery of protogyny in these genera, led Downie et al. (2002) and Sun et al. (in press) to propose it as evidence for a monophyletic origin of all perennial apioids of western North America. Here we provide evidence for protogyny in yet another, previously unexamined, western apioid genus: *Cymopterus*.

The systematics of the genus *Cymopterus* are in flux (Downie et al. 2002). As currently constituted, there are 35 to 45 species endemic to western North America, but the genus is now thought to be polyphyletic (Sun et al. in press). *Cymopterus beckii* Welsh & Goodrich, Pinnate Spring-parsley, is rare, categorized as a C2 sensitive species by the U.S. Fish and Wildlife Service. It is limited in distribution to several dozen occurrences on USDA Forest

Service and National Park Service land in Wayne and San Juan Cos. in central and southeastern Utah, and to a recently reported population in northern Navajo Co., Arizona (Holiday 2000). Species with C2 designations are potential prospects for listing under the U.S. Endangered Species Act, pending judgments based upon the collection of additional information.

Among the important subjects to investigate for rare plants, is their mode of reproduction. If we are to devise meaningful conservation management programs, then one of the most pressing concerns is to learn how these plants create new recruits. Is sexual reproduction common, and, if so, is it enabled by pollinators? Pollinators come in numerous taxa, and it is important to identify them. These are questions we set out to answer for this rare umbellifer. In addition, we will describe the unusual flower maturation sequence, and provide data on flower sex expression and selected reproductive characteristics.

METHODS

Plants at three *C. beckii* occurrences in Capitol Reef National Park, Wayne Co., UT were studied: Cohab Canyon (CO) (T29S R6E), T & E Canyon (TE) (T29S R6E), and Van Belle's Canyon (VB) (T30S R7E). All are narrow, rocky and sandy canyons in pinyon-juniper-mountain brush communities that receive full sun for only a few hours per day.

To describe floral maturation, we selected and marked umbels in the very early stages of anthesis from several plants at TE and VB. We recorded the sequence of development of all florets in the chosen umbels for several consecutive weeks. Additionally, at all three sites, we counted staminate and pis-

¹ Author for correspondence, e-mail: andrena@biology.usu.edu

TABLE 1. THE AVERAGE NUMBER (\pm STANDARD DEVIATION) OF UMBELLETS, FLOWERS PER UMBELLET, AND PERCENT PISTILLATE FLOWERS ACCORDING TO INNER AND OUTER POSITION IN *CYMOPTERUS BECKII* IN CAPITOL REEF NATIONAL PARK, UTAH. N = 26 for total umbellets; N = 19 for others.

| | Umbellets | Flowers/ umbellet | % Pistillates |
|-------|-----------|----------------------|---------------|
| Outer | 4.7 (0.7) | 11.7 (1.1) | 52.4 (8.4) |
| Inner | 2.8 (1.1) | 8.4 (1.5) | 10.4 (11.2) |

tillate flowers on two to four umbels of randomly selected plants.

We collected flower-visiting insects in 2002 with a butterfly net on May 14 and 23 at CO; on seven days from May 8 to June 18 at TE; and on seven days from May 10 to June 25 at VB. Four 30-minute collection periods were spaced throughout each day.

RESULTS

Flower Development and Umbel Sex Expression

The inflorescences of *C. beckii* are compound primary umbels organized into peripheral (outer) and central (inner) umbellets (see also Lovett Doust 1980; Lindsey 1982) of five to fifteen flowers each. Inflorescences with secondary umbels are rare (we found only one in an intensive search). Each umbellet contains either fructiferous pistillate and staminate flowers, or only staminate flowers. Pistillate flowers have two styles; all flowers have three to five stamens. The pistillate flowers occur primarily on the periphery of the outer umbellets and uncommonly in inner umbellets.

Pinnate Spring-parsley exhibits multicycle dichogamy (Lloyd and Webb 1986). Genets produce multiple compound primary umbels, a few of which may reach anthesis in synchrony. However, most umbels are produced in succession rather than in synchrony. Thus, some geitonogamous selfing is possible.

Individual umbels are both intra- and interflorally protogynous; female reproductive parts develop first throughout the umbel and wilt before any stamens mature. The outer pistillate flowers in the outer umbellets are first to reach anthesis. When the styles of pistillates in the outer umbellets are fully developed, the styles of any pistillates in the inner umbellets are approximately half developed. When the styles of the pistillates are developing the flower is still green. As the styles wilt, the stamens of both the pistillate and staminate flowers begin to develop and turn yellow. Like female function, development of staminate function is somewhat retarded in inner umbellets. Thus, Pinnate Spring-parsley would seem to be a clear example of the type of dichogamy that Cruden and Hermann-Parker (1977) termed "temporal dioecism" and Lloyd and Webb

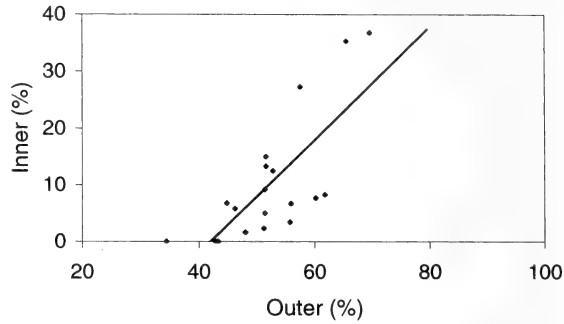


FIG. 1. The percentage of pistillate flowers in inner and outer flowers of 19 *Cymopterus beckii* umbels in Capitol Reef National Park ($y = 0.99x - 41.7$; $r^2 = 0.57$; $P = 0.002$).

(1986) termed "synchronous" wherein there is little or no overlap in gender within an umbel.

Outer umbellets of *C. beckii* umbels are significantly more numerous than inner umbellets (Table 1, paired t-test, $t = 8.4$, $df = 25$, $P < 0.001$). Outer umbellets also produce slightly, but significantly, more flowers than do inner umbellets (paired t-test, $t = 7.5$, $df = 18$, $P < 0.001$). And finally, there is a highly significant difference in percent pistillate flowers between inner and outer umbellets (paired t-test, $t = 24.9$, $df = 18$, $P < 0.001$): only about 10% of the flowers of inner umbellets are pistillate (an average of nine staminate per pistillate), while over 50% of flowers of outer umbellets are pistillate. There is also a strong positive association between the percentage of pistillate flowers in the inner and outer umbellets (Fig. 1): plants whose outer umbellets have high percentages of pistillates also have more pistillates in their inner umbellets. Using the estimates from Table 1, we calculate that the average *C. beckii* umbel produces about 75 flowers, of which approximately 40% are pistillates. We sexed flowers of marginally asynchronous umbels on a limited sample of genets ($n = 5$) and detected no difference in gender ratios between them. Thus, the average overall umbel gender ratio is about 1.5 staminate per pistillate which is substantially lower than the 4:1 ratio reported for some other species (e.g., Lovett Doust 1980). Interestingly, the 1.5 ratio is virtually identical with those reported for secondary and tertiary umbels for the closely related *Pseudocymopterus montanus* (Schlessman and Graeffe 2002).

Pollinators

Although flowers of *C. beckii* were visited only infrequently, a diverse array of small insects were collected and observed. Bees appeared to be the most important visitors; small native sweat bees (Halictidae) were most evident (Table 2). In particular, two species of *Dialictus* and one of *Evylaeus* were present at all three sites and are the most likely pollinators although only one *D. petrellus* female

TABLE 2. BEE SPECIES (GROUPED BY FAMILY) CAPTURED ON THE FLOWERS OF *CYOPTERUS BECKII* AT THREE SITES IN CAPITOL REEF NATIONAL PARK, UTAH. *Hylaeus (Paraprosopidis)* n. sp. is an undescribed species.

| | CO | TE | VB |
|--|----|----|----|
| Colletidae | | | |
| <i>Hylaeus (Paraprosopidis)</i> n. sp. | | X | |
| Halictidae | | | |
| <i>Dialictus petrellus</i> | X | X | X |
| <i>Dialictus</i> sp. | X | X | X |
| <i>Evyllaeus pulveris</i> | X | X | X |
| <i>Lasioglossum heterorhinum</i> | | | X |
| Megachilidae | | | |
| <i>Ashmeadiella cactorum</i> | | | X |
| Total Specimens Collected | 18 | 37 | 37 |

carried *Cymopterus* pollen. The bees only visited *C. beckii* flowers during the few hours when the plants were insolated. Other miscellaneous dipterans (n = 53), coleopterans (n = 59) and hymenopterans (wasps, n = 15) were also captured but all lacked *Cymopterus* pollen. Our results parallel those of Lindsey (1984) who also found a few species of bee pollinators and many miscellaneous insect visitors to flowers of *Thaspium* and *Zizia* species.

DISCUSSION

Our observations on the dichogamous floral development of Pinnate Spring-parsley suggest that pistillate flowers cannot produce seeds unless insects move pollen from a staminate stage umbel to a female stage umbel. The pollen may be from another genet, or, if *C. beckii* is self-compatible like most umbellifers (Bell 1971), from a staminate flower in another umbel on the same genet. The need for pollen movement is supported by preliminary bagging experiments at VB: no schizocarps were formed on 13 of 14 bagged umbels, and only one schizocarp was produced on the other. This conclusion is somewhat tenuous, however, because three of eight bagged umbels at TE produced 34 schizocarps. Either plants at VB and TE differ in breeding system, or more likely, insects gained access to the three umbels at TE. Additional studies are required to clarify the issue.

The facilitators of pollination of *C. beckii* remain unclear. Like Schlessman (1982), Lindsey (1984), and Schlessman and Graceffa (2002), who studied other apioids, we found numerous incidental dipterans, coleopterans, wasps and a few bee species visiting *C. beckii* flowers. Kaye (1992) reported that a few fly, wasp and beetle taxa, in addition to bees, seemed to transport pollen from flower-to-flower in *Lomatium bradshawii*. We found no pollen on any of our non-bee visitors and only on one of our collected bees. Bees were mostly members of the Halictidae, most of which visit a wide variety of flow-

ers for pollen and nectar throughout much of the western U.S. Unlike Lindsey (1984) we failed to find any pollinators specialized on the Apiaceae, with the possible exception of an unidentified species of *Dialictus* about which little is known. We agree with the assessment of Schlessman and Graceffa (2002) that additional studies are needed to elucidate the mechanisms and agents of pollination in apioids.

Cymopterus beckii differs from other typical protogynous species of western apioids (Downie et al. 2002) in that it produces only compound primary umbels while other taxa produce secondary and tertiary umbels as well (Schlessman 1978, 1982; Lindsey 1982; Webb 1984; Schlessman and Graceffa 2002). Its primary umbel is also unlike the primaries of other western apioids in gender composition; rather than containing mostly staminate flowers, it contains approximately 40% pistillates and thus most closely resembles the secondary or tertiary umbels of other protogynous taxa. *Lomatium* (Schlessman 1978, 1982), *Thaspium* and *Zizia* (Lindsey 1982), *Myrrhidendron* (Webb 1984), and *Pseudocymopterus* (Schlessman and Graceffa 2002) all produce compound umbels in which the first-flowering primary produces few (sometimes no) pistillate flowers. It is as if Pinnate Spring-parsley has lost, or never evolved, the staminate primary umbel; because of this it may be the most extreme example of protogyny in apioids described thus far.

Several explanations have been offered for protogyny in andromonoecious umbellifers without attaining a satisfactory resolution (see, most recently, Bertin 1993; Bertin and Newman 1993; Schlessman and Graceffa 2002; Schlessman and Barrie in press); we intend only to "throw our oar" into the "shallow end of this pond". Currently, the most favored hypotheses appear to be reproductive assurance (protogyny more than protandry is thought to improve chances of selfing when pollinators are scarce, e.g., Bertin 1993; Schlessman and Barrie in press) and pollinator specialization (the development of specialized floral parts, associated only with protogyny, that restrict nectar harvesting to specific pollinators (Bell 1971; Webb 1984; Schlessman and Barrie in press)). We are skeptical that either of these explanations apply to *C. beckii* (and perhaps to other species as well); to argue that reproductive assurance is greater with protogyny than with protandry requires a demonstration that stigma receptivity in protogynous species extends into the period of anther dehiscence, but that in protandrous species no viable pollen remains when stigmas become receptive. We know of no such proof for any umbellifer. The second favored hypothesis, pollinator specialization, seems not to apply to the very small and easily plundered *C. beckii* flowers.

Instead, we think protogyny in *C. beckii*, with its pistillate-containing primary umbel, is best understood as a system to encourage outbreeding (Webb

1981) and minimize intra-umbel selfing (Bertin 1993), while not excluding reproductive assurance via inter-umbel selfing. Insects landing on a female stage flower can only effect pollination if they carry pollen from another umbel. In many cases, especially early in the flowering season, this would necessarily be an umbel from another genet. Other factors, such as avoidance of interference between genders (Lloyd and Webb 1986; Bertin 1993; Bertin and Newman 1993) may also favor protogyny because it appears easier to move relatively slender styles out of the way of subsequently maturing large, plump anthers, than vice-versa.

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THE SYSTEMATIC SIGNIFICANCE OF COLOR VARIATION IN
MONOTROPA HYPOPITHYS (ERICACEAE) INFERRED FROM LARGE
RIBOSOMAL SUBUNIT (26S) rRNA GENE SEQUENCES

RAY NEYLAND

Department of Biological and Environmental Sciences, McNeese State University,
Lake Charles, LA 70605
rneyland@mcneese.edu

ABSTRACT

Monotropa hypopithys is a non-photosynthetic myco-heterotrophic herb. Early-season forms tend to be wholly yellow and late-season forms often exhibit red pigmentation. Color variation often has been used to distinguish taxonomic segregates, and it has been proposed that yellow forms are genetically distinct from red forms. However, evidence from 26S large ribosomal subunit rRNA gene sequences suggests that red and yellow forms have not evolved along separate lines of descent.

Key Words: *Monotropa hypopithys*, Monotropoideae, Monotropeae, plant systematics.

Commonly called Pinesap, *Monotropa hypopithys* L. is a non-photosynthetic myco-heterotrophic herb (Furman and Trappe 1971) that obtains fixed carbon from basidiomycete ectomycorrhizal *Tricholoma* fungi (Bidartondo and Bruns 2002). The species is widely distributed in Eurasia and North America (Thorne 1972; Hultén and Fries 1986) and has the widest geographical distribution of any other member of the Monotropoideae (Olson 1993; Bidartondo and Bruns 2002). *Monotropa hypopithys* is not threatened or endangered, at least in the United States (U.S. Fish and Wildlife Service 1999).

The taxonomy of *M. hypopithys* is confused. Although some authors recognize only the single species *M. hypopithys* (e.g., Kamienski 1881; Domin 1915; Copeland 1941; Gupton 1962; Wallace 1975; Kartesz 1994), at least 85 synonyms have been published (Wallace 1975). Additionally, although most authors have placed this taxon within the genus *Monotropa*, others have segregated it in *Hypopitys* (e.g., Rafinesque 1810; Bicknell 1914; House 1923; Small 1933; Furman and Trappe 1971).

At higher levels, *M. hypopithys* has been positioned in family Monotropaceae (e.g., Bicknell 1914; Small 1914; Cronquist 1968; Kartesz 1994). Alternatively, it has been placed in subfamily Monotropoideae either in family Ericaceae (e.g., Copeland 1941; Stevens 1971; Wallace 1975; Kron et al. 2002) or the family Pyrolaceae (e.g., Drude 1889; Lawrence 1965; Furman and Trappe 1971).

Various characters have been used to distinguish segregates of *M. hypopithys*. For example, Hultén and Fries (1986) recognized three subspecies corresponding to geography. An analysis based on plastid *rps2* and nuclear rDNA (28S and ITS) sequences by Bidartondo and Bruns (2001) suggested that Eurasian and North American *M. hypopithys* are polyphyletic. That finding is consistent with the cytological evidence of Löve (1954) who reported

that European representatives are $2n = 16$ and that North American representatives are $2n = 32$. Additionally, Takahashi (1987) reported that plants native to the New World produce two-colporate pollen grains; however, plants native to the Old World produce three-colporate pollen grains.

Plant coloration, including stem, bracts and perianth, also has been used as a factor in naming segregates of *M. hypopithys* (Fernald 1950; Gupton 1962). Examples include Torrey (1843), Bicknell (1914), Small (1914) and Seymour (1969). Although they provided no specific evidence, Niering and Olmstead (1979) stated that the red and yellow forms are genetically different. Additionally, color has been reported to correlate with time of flowering. Specifically, earlier-season forms tend to be wholly yellow and later-season forms often exhibit red pigmentation (Torrey 1843; Fernald 1950; Gupton and Swope 1979; Thieret et al. 2001).

The specific chemical composition of the respective red and yellow pigments of *M. hypopithys* has not been described. However, the carotenoids lutein and β -carotene have been identified by Neamtu and Bodea (1971). Although flavonoid pigments were reported absent (Bohm and Averell 1989), Harborne and Williams (1973) found quercetin in hydrolysed extracts of *M. hypopithys* and Funk (1937) found anthocyanin in the red form designated as *M. hypopithys* var. *sanguinea* Hausskn.

Because color has been reported to be correlated with time of flowering, red and yellow forms of *M. hypopithys* may be reproductively isolated and therefore, genetically distinct as suggested by Niering and Olmstead (1979). The purpose of this study was to test the hypothesis that red and yellow forms of *M. hypopithys* are phylogenetically distinct from each other. This investigation was made by phylogenetic inference using large ribosomal subunit (26S) rRNA gene sequences. The 26S gene was used in this study because it has been shown to exhibit a

TABLE 1. TAXA USED IN THIS STUDY. All representatives are from subfamily Monotropoideae (*sensu* Kron et al. 2002). Ingroup members are from tribe Monotropeae. Outgroup members are *Pterospora andromedea* (tribe Pterosporaeae) and *Chimaphila maculata* (tribe Pyroleae). Voucher numbers and GenBank accession numbers are indicated. Vouchers are housed at McNeese State University (MCN). DNA supplied by Martin Bidartondo was used to sequence the OR2359 representative of *Monotropa hypopithys*. Although no herbarium voucher exists for this specimen, frozen material is maintained at The University of California, Berkeley.

| Taxon | Collection location | Form/date of collection at anthesis | Voucher | GenBank accession |
|---------------------------------------|-------------------------------------|-------------------------------------|-------------------------|-------------------|
| <i>Monotropa hypopithys</i> L. | | | | |
| NM2037 | Lincoln County, NM | Red/8-15-02 | Neyland 2037 | AF543835 |
| MA2052 | Middlesex County, MA | Yellow/8-2-02 | Neyland 2052 | AY166966 |
| CN2046 | Tolland County, CT | Red/8-28-02 | Neyland 2046 | AY166968 |
| CN2080 | Tolland County, CT | Yellow/7-28-03 | Neyland 2080 | AY373260 |
| CN2048 | Litchfield County, CT | Yellow/8-28-02 | Neyland 2048 | AY166967 |
| OR2359 | Lane County, OR | Red/6-27-00 | — | AY205316 |
| <i>Monotropa uniflora</i> L. | | | | |
| LA 1954 | Natchitoches Parish, LA | | Neyland & Hennigan 1954 | AF540062 |
| CR2066 | Cordillera de Talamanca, Costa Rica | | Neyland 2066 | AY221084 |
| <i>Chimaphila maculata</i> (L.) Porsh | Union County, GA | | Neyland 2049 | AY294625 |
| <i>Pterospora andromedea</i> Nutt. | Grant County, OR | | Neyland 2078 | AY368156 |

level of divergence that is informative within subfamily Monotropoideae (Cullings 1994; Bidartondo and Bruns 2001).

METHODS

Collection information, voucher numbers and GenBank accessions for the taxa sequenced in this study are listed in Table 1. Taxonomy follows Kron et al. (2002). All representatives were from subfamily Monotropoideae (Ericaceae). Both red and yellow forms of *M. hypopithys* (tribe Monotropeae) were included in the ingroup. The outgroup consisted of *Chimaphila maculata* (tribe Pyroleae) and *Pterospora andromedea* (tribe Pterosporaeae).

Monotropa hypopithys individuals were selected from several sites within the United States (Table 1). Three representatives from Connecticut included red (CN2046) and yellow (CN2080) forms growing sympatrically as well as another yellow form (CN2048) collected about 51.2 km distant (Table 1). A red representative from Oregon (OR2359) and one from New Mexico (NM3037) and a yellow representative from Massachusetts (MA2052) also were included (Table 1).

An approximate 1 kb DNA segment of the 26S gene from each representative was used in this study. This segment, which spans base positions 4–950 in *Nicotiana tabacum* (GenBank Accession AF479172), is characterized by conserved segments and variable expansion segments (Kuzoff et al. 1998).

Total DNAs were extracted from tissue using the CTAB method of Doyle and Doyle (1987). DNA sequences were amplified via polymerase chain reaction (PCR) (Mullis and Faloona 1987) with combinations of forward and reverse primers referenced in Neyland (2002). Amplification was achieved with Tfl enzyme (Epicentre Technologies, Madison, WI), using the following thermocycling protocol: a hot start at 94°C for 3 min; 30 amplification cycles of 94°C for 1 min, 55°C for 1 min; 72°C for 3.5 min, a terminal extension phase at 72°C and an indefinite terminal hold at 4°C. The double-stranded PCR product was purified with QIAquick (Qiagen, Hilden, Germany) using the manufacturer’s protocol. Two µl of each sample were electrophoresed in a 1.0% agarose mini-gel for quantification against a known standard. Automated sequencing was conducted on an ABI Prism 377 Sequencer with XL Upgrade (housed at Louisiana State University, Baton Rouge, LA, USA) using ABI Prism, Big Dye Terminator cycle sequencing protocol (P.E. Applied Biosystems, Foster City, CA, USA). Sequences have been deposited in the GenBank database (Table 1).

Phylogenetic analysis was performed using the exhaustive search algorithm with Phylogenetic Analysis Using Parsimony (PAUP version 4.0b10) software (Swofford 2002). Absolute pair-wise nucleotide distances were calculated using PAUP.

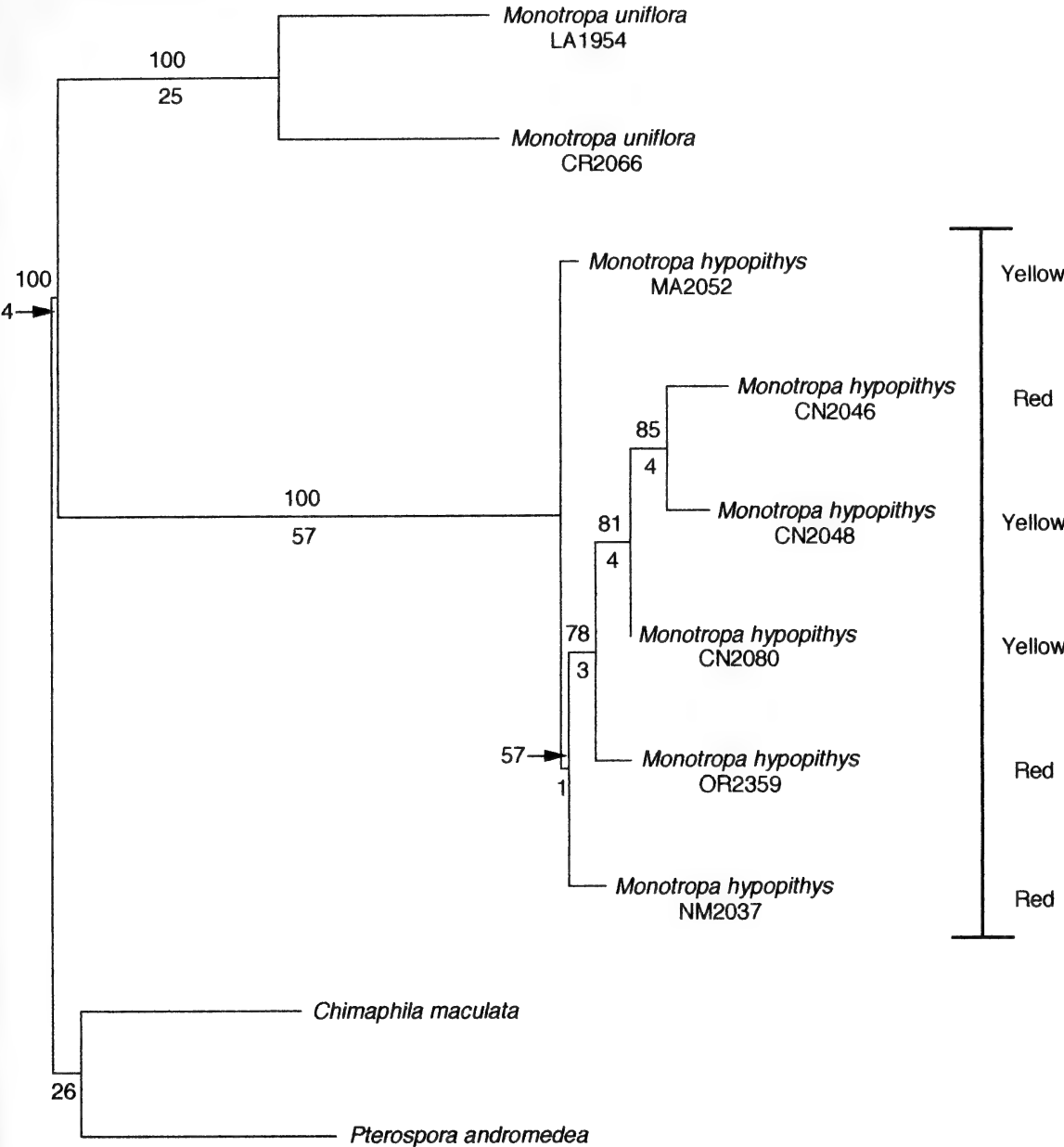


FIG. 1. Phylogram of the single most-parsimonious tree discovered from an exhaustive search using 26S rRNA gene sequences. The number of unequivocal synapomorphies is indicated below each branch. Bootstrap values are indicated above each branch. Color form is indicated in the side legend.

Disk copies of aligned sequences are available from the author.

As a measure of clade stability or robustness, bootstrap support (Felsenstein 1985) was calculated. Ten thousand bootstrap replications were employed in this analysis (MulTrees option in effect).

RESULTS

Sequences were easily aligned manually. Gaps were introduced to accommodate 14 single-point

insertions/deletions (INDELS) in the data set. The exhaustive search resulted in a single most-parsimonious tree (Fig. 1) of 175 steps with a consistency index of 0.9029 and a retention index of 0.8976.

Absolute distances within the entire data set range from a minimum of 7 between *M. hypopithys* (NM2037) and *M. hypopithys* (MA2052) and a maximum of 97 between *Pterospora andromedea* and *M. hypopithys* (CN2056 and CN2048).

DISCUSSION

Based on the recovered topology, red and yellow forms of *M. hypopithys* have not evolved along separate lines of descent. Specifically, clustering of like-colored individuals is not evident in the phylogram (Fig. 1).

The question remains as to why different color forms of *M. hypopithys* are produced. One possible explanation is that the fungal symbiont may play a role. Per Bidartondo and Bruns (2001) there is extreme specificity between *M. hypopithys* and its fungal host. However, ITS sequence data show no correlation between any particular fungal symbiont and color in *M. hypopithys* (Bidartondo personal communication).

Another possible explanation is that different color forms optimally attract different pollination vectors at different times of the year. Although no detailed pollination studies have been undertaken, Knuth (1909) posited that an insect would have to have a proboscis at least 1 cm long to reach the nectar in *M. hypopithys*. Knuth reported that he observed a female bee, *Bombus agrorum*, pollinating *M. hypopithys* and noted that the proboscis in this bee species is 10–15 mm long. However, Hagerup (1954) stated that he had never seen insects pollinating *M. hypopithys* flowers. Additionally, he noted that the flowers are designed for autogamy in that the anthers are positioned directly onto the stigma. Hagerup also noted that the flowers are fragrant with plainly visible nectaries which suggests that they are adapted for insect pollination as well. Although he did not confirm that ants are pollinating vectors, Gupton (1962) reported that they frequently have been observed on *M. hypopithys*.

Field observations by Wallace (1975) suggest that a correlation between color and time of anthesis may be illusory in *M. hypopithys*. Specifically, he reported that pink fruiting specimens occurred near reddish budding specimens and yellow blooming specimens and attributed this to the continuous development of adventitious buds on the perennial root system. However, Wallace's (1975) observations do not explain the relationship among the Connecticut representatives included in this study. Specifically, the yellow (CN2048) representative from People's Forest, Litchfield County is more closely related to the red (CN2046) from Shemipist Forest, Tolland County than it is to the yellow form (CN2080) from Shemipist Forest. That is, the red CN2046 is more closely related to the yellow CN2048 (collected 51.2 km distant) than it is to its sympatric yellow CN2080. The close relationship between the nonsympatric yellow CN2048 and the red CN2046 is strongly supported by a 85% bootstrap value (Fig. 1) and by one unique point insertion and one unique point deletion. Additionally, the bloom time for both CN2048 and CN2046 is near the end of August (Table 1). However, the bloom time for CN2080 is near the end of July.

Therefore, the sympatric CN2046 and CN2080 may be reproductively isolated. Although this relationship suggests that color alone is not a reliable indicator of systematic distinction in *M. hypopithys*, it also suggests that at least some level of molecular divergence may be present in sympatric red and yellow subpopulations, at least in Shemipist Forest.

An adequate explanation for color variation in *M. hypopithys* has yet to be established. Although the molecular data from the present study suggests that the red and yellow forms have not evolved along separate lines, these data do not explain why different color forms of *M. hypopithys* are produced. Additional molecular data may help explain this phenomenon. For example, because color is variable at the population level, an ideal approach would employ at least two different colored plants from several populations using sequences from several genes. Traditional field observations, especially pollination studies, also may prove illuminating.

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TEMPORAL VARIATION IN LONGEVITY OF *OPUNTIA ENGELMANNII*
(CACTACEAE) FLOWERS

JANICE E. BOWERS

U.S. Geological Survey, 1675 West Anklam Road, Tucson, AZ 85745
jebowers@usgs.gov

ABSTRACT

Flower longevity interacts with other variables such as pollinator visitation and plant resources to control fruit set and seed production of many flowering plants. This study examined temporal patterns of floral longevity for *Opuntia engelmannii* Salm-Dyck. (Engelmann prickly-pear), a shrubby cactus common in the northern Sonoran Desert. Observations made at Tumamoc Hill, Tucson, AZ, USA, demonstrated that the flowers can open on a single day or two consecutive days. On average, one-day flowers opened at 1100 hr and closed 5.5 hr later at 1630 hr (MST). Flowers that bloomed on two consecutive days were open altogether for an average of 12.2 hr. Their first day of bloom lasted about 6.5 hr, beginning around 1000 hr and ending at about 1630 hr; on their second day, two-day flowers opened at 0830 hr and closed shortly after 1400 hr. The proportion of two-day flowers in the population was inversely related to maximum temperature on the first day of bloom and minimum temperature between the first and second days of bloom. Flowers opening in the afternoon were more likely to bloom a second day than those opening in the morning. Flowers open for the second time offered significantly less nectar and pollen than freshly opened flowers; nevertheless, rewards on the second day were high enough to encourage visitation by potential pollinators. Patterns of daily opening and closing appeared well suited to reducing the risk of poor or no pollination.

RESUMEN

La longevidad de flores se relaciona con otros factores como visitas de polinizadores y recursos de la planta para regular la producción de frutas y semillas. Esta investigación examina los patrones temporales de longevidad en flores de *Opuntia engelmannii* Salm-Dyck. (el nopal de Engelmann), un cactus común del norte del Desierto Sonorense. Observaciones en Tumamoc Hill, Tucson, Arizona, EEUU, demuestran que las flores se abren un o dos días. Flores que abren por solo un día abrieron a las once de la mañana y cerraron a las cuatro y media de la tarde. Las que florecen por dos días seguidos se quedaron abiertos por un promedio de 12.2 horas en total. Su primer día de floración duró ~ 6.5 horas, comenzando a más o menos las diez de la mañana y terminando a más o menos las cuatro y media de la tarde. En su segundo día las flores de dos días abrieron a las ocho y media de la mañana y cerraron poco después de las dos de la tarde. El porcentaje de las flores de dos días en la población está relacionado inversamente con la temperatura máxima en el primer día de floración y la temperatura mínima entre los dos días de floración. Las flores que abren por la tarde fueron más probables de durar dos días que esas que abren por la mañana. Las flores abiertas en su segundo día tuvieron menos néctar y polen que flores recién abiertas. Sin embargo, el néctar y polen en el segundo día fueron suficiente abundante para alentar las visitas de polinizadores potenciales. Patrones de abrir y cerrar a diario parecen bien apropiados para reducir el riesgo de polinización inadecuada.

Key Words: Cactaceae, floral biology, floral longevity, *Opuntia engelmannii*, Sonoran Desert.

Flower longevity, the period of time from anthesis to senescence, interacts with other variables such as pollinator visitation and plant resources to control fruit set and seed production of many flowering plants (Primack 1985; Ashman and Schoen 1996). Large flowers, such as those typical of the Cactaceae, are presumably expensive to maintain for more than a single day and should open a second day only if there is ultimately a strong benefit to doing so, such as increased fruit set, seed production, or pollen donation (Primack 1985; Ashman and Schoen 1996). Proximate factors that influence longevity include transpirational water loss, respiration rate, and pollinator abundance (Primack 1985; Rosas and Pimienta 1986; Ashman and Schoen 1996).

Flowers of *Opuntia engelmannii* Salm-Dyck. (Engelmann prickly-pear), a shrubby platyopuntia widespread throughout the southwestern United States, are believed to last a single day (Parfitt and Pickett 1980; Turner et al. 1995), but floral longevity of two days has been reported for at least five other platyopuntias (Rosas and Pimienta 1986; Osborn et al. 1988; Schlindwein and Wittmann 1997). In these species, one-day flowers open in the morning and close permanently in late afternoon of the same day; two-day flowers open in the afternoon of their first day and close after several hours, then open again the following morning for several hours before senescing (Osborn et al. 1988; Schlindwein and Wittmann 1997). Both types last approximately the same amount of time, 6 to 12 hr (Osborn et al.

1988; Schlindwein and Wittmann 1997). The objective of this study was to describe temporal patterns of floral longevity for *O. engelmannii*. Specific questions asked were: (1) do individual flowers open on consecutive days, (2) is floral longevity consistent throughout the flowering season and among years, (3) is floral longevity limited by environmental or intrinsic factors, and (4) do pollen and nectar rewards vary with floral longevity?

METHODS

Study Area

The study site was located at 720 m above sea level at the base of Tumamoc Hill (32°13'N, 111°05'W), an outlier of the Tucson Mountains, Pima County, AZ, USA. Study area vegetation is characteristic of the Arizona Upland subdivision of the Sonoran Desert (Shreve 1951). In addition to *O. engelmannii*, dominant plants include *Cercidium microphyllum* (Torr.) Rose & Johnst., *Ambrosia deltoidea* (A. Gray) Payne, *Acacia constricta* Benth., *Larrea tridentata* (Moc. & Ses.) Cav., *Krameria grayi* Rose & Painter, *Carnegiea gigantea* (Engelm.) Britton & Rose, *Ferocactus wislizenii* (Engelm.) Britton & Rose and *Opuntia leptocaulis* DC. Annual precipitation (300 mm) is seasonally distributed as a highly variable winter-early spring (November to March), an arid foreshummer (April to June), a predictable summer monsoon (July to August), and a highly variable autumn (September to October). Maximum temperatures in summer often exceed 40°C. Minimum temperatures rarely drop below -6°C in winter. Although freezing nights can be frequent in winter, daytime temperatures always rise above 0°C.

Study Species

Opuntia engelmannii blooms once a year in April and May (Kearney and Peebles 1960; Turner et al. 1995). The hermaphroditic, yellow flowers are bowl-shaped and have a diameter of 6 to 9 cm (Benson 1982). Nectar accumulates in a short floral tube above the inferior ovary. Nectar production is high relative to other *Opuntia* spp. in the southwestern United States (Grant et al. 1979; McFarland 1983; Osborn et al. 1988; Neff and Simpson 1992). Anthers are numerous and produce copious pollen. As in many *Opuntia* species, the stamens are thigmotropic (Parfitt and Pickett 1980). Across the range of the species, flower visitors include several species of solitary bees (Grant and Hurd 1979; Grant and Grant 1979; Parfitt and Pickett 1980; Osborn et al. 1988). The anthophorids *Diadasis rinconis* Cockerell and *D. opuntiae* Cockerell are probably the most frequent pollinators in southern Arizona (Buchmann personal communication). Before the fruits ripen, beetles are common flower herbivores (Grant and Connell 1979).

Data Collection and Analysis

Two pilot studies were undertaken to determine whether individual flowers of *O. engelmannii* open on consecutive days. On 26 April 1995, 19 flower buds on seven plants and 21 open flowers on 10 plants were tagged and visited daily for the next seven days to monitor opening and closing dates. In 1997, additional flowers were marked and monitored on 18 April ($n = 15$ flowers) and 1 May ($n = 129$ flowers). Color and condition of tagged flowers were noted at each visit to determine how the appearance of flowers changed over time. In this and the following studies, flowers were tagged with numbered plastic or aluminum tags secured with straight pins inserted either into the base of the ovary or into the cladode beside the ovary. Mucilage quickly sealed the slight wound created by the pin. Flowers appeared unaffected by the pins.

Longevity in hours of one- and two-day flowers was monitored in 2003. Observations were made early in the flowering season (17 and 18 April) and about midway through the season (28 April to 2 May). Altogether, 192 flower buds on five plants were tagged on the day they opened for the first time. Buds were monitored every two hours throughout that day and the next from 0830 to 1630 hr (MST), and times of opening and closing were recorded. Independent t-tests were used to compare the longevity in hours of one- and two-day blossoms. A χ^2 -test was used to determine whether opening time (morning versus afternoon) on the first day of bloom differed between one- and two-day flowers.

Proportions of one- and two-day flowers in the population were determined in 2000 and 2001 ($n = 16$ plants). In 2000, all flower buds ($n = 580$) were tagged at the start of the flowering season and monitored twice daily to determine longevity in days and also approximate time of opening (morning or afternoon). In 2001, the large number of flower buds (>4500) made it impracticable to individually tag and monitor all of them. Instead, the proportion of two-day flowers was estimated by making daily counts of total number of fresh flowers and number of flowers open for the second time on each sample plant. Counts were made in the morning, when second-day flowers (orange perianth) could be readily distinguished from fresh flowers (yellow perianth) (see Results). The proportion of second-day flowers was calculated as orange flowers of the current day divided by yellow flowers of the previous day. In addition, >200 flower buds were tagged and monitored twice daily in 2001 to determine approximate time of opening. Regression analysis was used to examine the influence of air temperature on the proportion of flowers opening a second day in 2000 or 2001. Maximum and minimum daily temperature were used separately as independent variables. Temperature data came from the University of Arizona, about 6 km distant.

To better understand daily and seasonal patterns of visitation, visits by potential pollinators were monitored throughout the flowering season in 2000 ($n = 90$ flowers) and 2001 ($n = 261$ flowers). Flowers were watched for 10 minutes, during which time the number of bee visitors was recorded. No attempt was made to identify the bees. Most observations were made between 0800 and 1300 hr (MST), when pollinators were very active. Beetles, which are not effective pollinators of cactus flowers (Grant and Connell 1979), were not included in these surveys.

Pollen and nectar contents of first- and second-day flowers were examined to see whether visitors can obtain rewards from older flowers. On 29 April 2001, mass of pollen was measured in freshly opened flowers and in flowers open for the second consecutive day. Twenty-four flowers on four plants were cut at 1030 hr and brought into the laboratory. Pollen was collected on sheets of waxed paper by holding flowers upside down over the paper and tapping them. Additional pollen was collected by dusting the anthers and petals with a small sable-hair brush. Pollen and paper were weighed together to the nearest 1.0 mg, then the waxed paper, cleaned of pollen, was weighed separately. The mass of pollen grains was calculated by subtraction.

Standing crop nectar in first- and second-day flowers was sampled in 1998. On 9 May, 11 May, and 12 May, flowers were tagged and classified according to color, condition, and time of opening as: (1) first day of bloom, opening in the morning ($n = 32$ flowers), (2) first day of bloom, opening in the afternoon ($n = 24$ flowers), or (3) second day of bloom, opening in the morning ($n = 48$ flowers). Nectar was sampled at hourly intervals on 9 May (0700 to 1100 hr), 11 May (0800 to 1600 hr), and 12 May (0700 to 1100 hr). Flowers were placed in plastic bags as they were removed from the plant, and the batch was refrigerated within several minutes. Nectar contents were measured in the laboratory within an hour of collection. Flower nectar was extracted using a bulb and uncalibrated glass pipette, then measured to the nearest 0.1 μl using a digital micropipette. Nectar values from all three days were pooled and averaged within hourly intervals.

RESULTS

The pilot studies demonstrated that *O. engelmannii* flowers can open on two consecutive days, although many do not. Of 40 flowers buds and flowers tagged early in the flowering season in 1995, all lived for two days. In 1997, the proportions of two-day flowers were 78% on 18 April and 25% on 1 May. Fresh flowers had bright a yellow perianth; in addition, their stamens were pressed together, and little or no pollen could be seen on the stigmas or petals. As the day advanced, petals turned orange, stamens diverged, and pollen be-

came liberally dusted on stigmas and petals. Flowers on their second day of bloom were also characterized by orange color, spreading stamens, and abundantly dispersed pollen. Flowers that opened in the morning typically senesced the same day; flowers that opened in the afternoon had a greater potential to bloom again the next day. From these findings, it was evident that: (1) a fresh flower opening in the morning is likely to be a one-day flower; (2) a fresh flower opening in the afternoon might be a one-day or a two-day flower; (3) a flower that has an orange perianth when it opens in the morning is a two-day flower on its second day of bloom. During the morning hours, therefore, it was possible to discern whether a flower was open for the first or second time and to predict its longevity with a fair degree of confidence.

In 2003, one-day flowers opened on average at 1100 hr (range = 0830 to 1230 hr) and closed 5.5 hr later at 1630 hr. Flowers that bloomed on two consecutive days were open altogether for an average of 12.2 hr. Their first day of bloom lasted about 6.5 hr, beginning around 1000 hr (range = 0830 to 1230 hr) and ending at about 1630 hr. On their second day, two-day flowers opened at 0830 hr without exception and closed shortly after 1400 hr. The difference in total longevity of one- and two-day flowers was significant ($t = 13.5$, $P = 0.001$). Note that daily phenology can be more variable than these data, gathered from four individuals over several days, would suggest. In other years, for example, some flowers opened for the first time as late as 1600 hr (personal observation).

In an analysis using all flowers tagged in 2003, one- and two-day flowers did not differ significantly in time of opening (morning versus afternoon) on the first day of bloom ($\chi^2 = 0.04$, $df = 1$, $P = 0.85$). This result was strongly influenced by the 28 flowers that bloomed for the first time on 17 April: all but two opened at 0830 hr, and all but three lasted two days. When these early-season flowers were dropped from the analysis, there was a significant difference in opening and closing times between one- and two-day flowers ($\chi^2 = 10.4$, $df = 1$, $P = 0.001$), with 70% of one-day flowers opening in the morning, and 71% of two-day flowers opening in the afternoon on their first day of bloom.

The proportion of flowers that opened on two consecutive days varied between years, being 0.8% in 2000 (4 of 483) and about 20% in 2001 (474 of 2368) (Fig. 1). In 2001, floral longevity was strongly associated with time of opening (morning versus afternoon): 93.7% of tagged flowers that opened in the morning ($n = 111$) turned out to be one-day flowers, and 56.9% of flowers that opened in the afternoon ($n = 102$) turned out to be two-day flowers ($\chi^2 = 64.1$, $df = 1$, $P = 0.001$). The number of two-day flowers in 2000 was too small for meaningful analysis; however, it is worth noting that

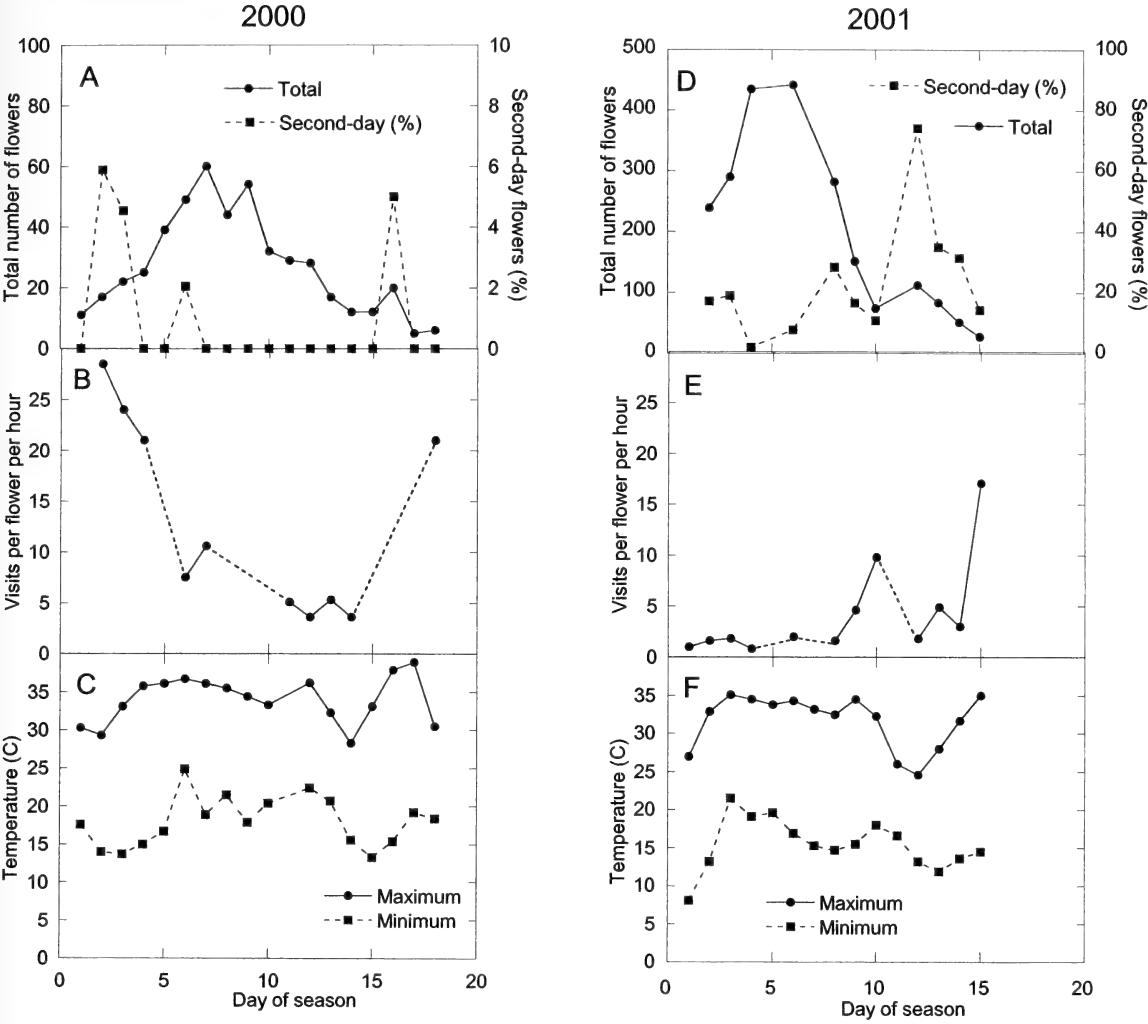


FIG. 1. The flowering season of *Opuntia engelmannii* in 2000 and 2001. Total number of flowers (circles) and proportion of two-day flowers (squares) in 2000 (A) and 2001 (D). Visits/flower/hour in 2000 (B) and 2001 (E); dotted lines show breaks in data collection. Daily maximum and minimum temperatures in 2000 (C) and 2001 (F).

88.8% of all flowers opened in the morning that year.

In 2001, there was a negative relation between temperature and the proportion of flowers that opened on two consecutive days. The relation was very strong for maximum temperature on the first day of bloom ($r^2 = 0.81$, $P < 0.001$) and not quite as strong for minimum temperature between the first and second days of bloom ($r^2 = 0.48$, $P = 0.01$) (Fig. 2a, b). In 2000, neither maximum nor minimum temperature were significantly related to proportion of two-day flowers, perhaps because most flowers opened in the morning; as noted above, flowers that open in the morning are likely to last only a single day.

Whether summarized by the day (Fig. 1) or by the hour (Fig. 3), visitation data were highly variable within and between years. Visits/flower/hr (\pm SD) in the morning were significantly higher in

2000 (11.2 ± 13.1) than in 2001 (4.2 ± 8.9) ($t = 5.59$, $P < 0.001$). The difference between years might have been related to intense competition among pollinators for flowers in 2000, a year of poor flower production, in contrast to 2001, a year of high flower production. Although afternoon observations were few, the trend in hourly visitation peaked in the morning and trailed off toward the afternoon (Fig. 3).

Mass of pollen grains (\pm SD) averaged 42 mg (± 16) and 20 mg (± 9) on the first and second days of bloom, respectively. The difference was significant ($t = 3.99$, $P = 0.001$) and undoubtedly reflected the time of day when flowers were harvested, about 1030 hr. At that time, flowers on their second day of bloom had been accessible to foraging bees for a longer time than recently opened flowers. The presence of pollen in second-day flowers indicated

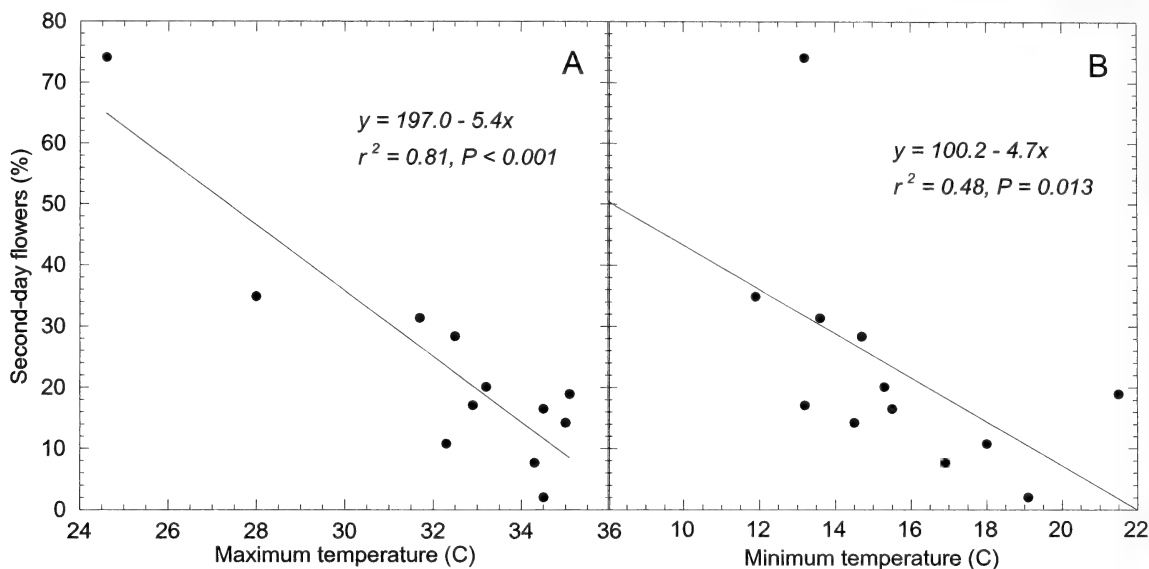


FIG. 2. Relation between air temperature and proportion of *Opuntia engelmannii* flowers that bloomed on two consecutive days in 2001. X axis represents maximum temperature on first day of bloom (A) or minimum temperature between first and second days of bloom (B).

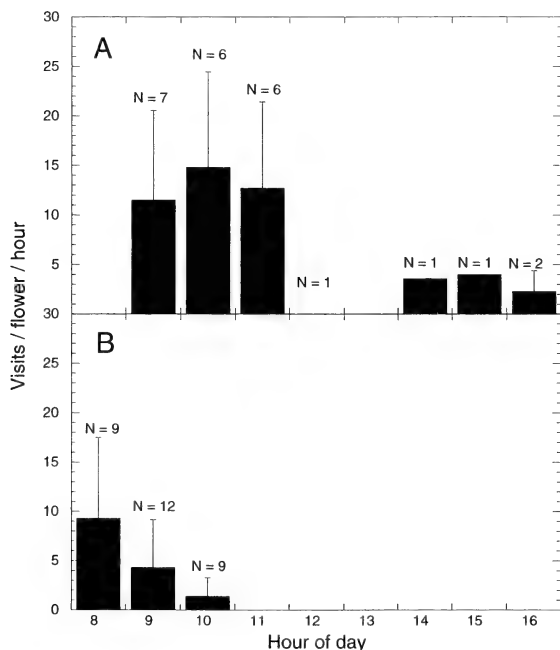


FIG. 3. Patterns of daily visitation (mean visits/flower/hr) by potential pollinators to flowers of *Opuntia engelmannii* in 2000 (A) and 2001 (B). Observations made throughout the flowering season were pooled and averaged within hourly intervals. N = days of observation. Error bars = 1 SD. In 2000, no observations were made from 0800 to 0900 hr or from 1300 to 1400 hr. In 2001, no observations were made after 1100 hr.

that some pollen remained at the end of the first day of bloom.

Day of bloom (first versus second) had a significant effect on standing crop nectar (ANOVA: $F = 7.6$, $df = 2, 12$, $P = 0.007$) (Fig. 4). On the first day of bloom, standing nectar crop averaged $22.6 \mu\text{l}/\text{flower}$ for flowers that opened in the morning and virtually the same, $21.9 \mu\text{l}/\text{flower}$, for those that opened in the afternoon. Flowers on their second day of bloom contained significantly less nectar than either of the other categories, only $11.9 \mu\text{l}/\text{flower}$ ($P < 0.02$). Note that although the reward was relatively small, pollinators could find nectar in some second-day flowers.

DISCUSSION

Flowers of *O. engelmannii* opened on one or two consecutive days. Pollen mass and nectar volume were significantly lower on the second day, yet remained high enough to reward flower visitors and encourage a low level of visitation. Whether flowers lived for one or two days depended in part on air temperature, with a higher proportion of flowers opening a second time after relatively cool days and nights (Fig. 2a, b). Assuming that floral stomates were open during the day, as seems to be the case for *Ferocactus cylindraceus* (Engelm.) Orcutt (Nobel 1977), the negative effect of high daytime temperatures on flower longevity likely reflected loss of moisture through increased evapotranspiration. Respiration also increases with temperature, and it seems likely that high respiration rates on warm days and nights reduced flower longevity as well. Given relatively cool temperatures, some or many

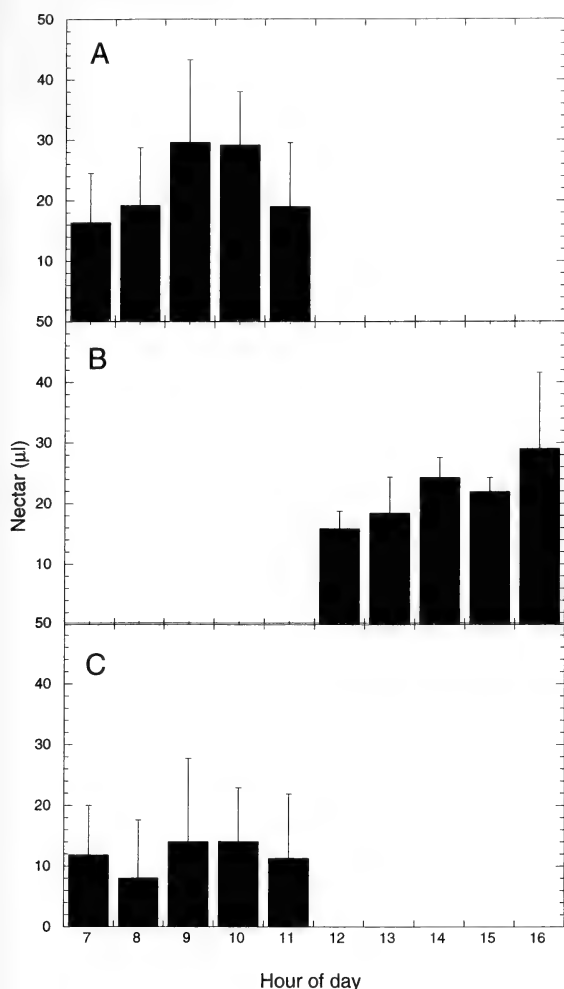


FIG. 4. Mean standing crop nectar of three phenophases of *Opuntia engelmannii* in 1998. (A) First day of bloom, flowers opening in the morning; (B) first day of bloom, flowers opening in the afternoon; (C) second day of bloom, flowers opening in the morning. Values represent the average amount of nectar measured in three to four flowers of each category at hourly intervals on three different days. Error bars = 1 SD.

flowers retained enough moisture to open two days in a row.

Another factor that determined how long flowers lived was time of opening. At mid-season in 2003, most (70%) two-day flowers opened in the afternoon, whereas most (71%) one-day flowers opened in the morning. In 2001, almost 94% of flowers that opened in the morning lasted a single day, and 57% of flowers that opened in the afternoon lived for two days. On their first day, two-day flowers opened about the same time as one-day flowers, but on their second day, two-day flowers typically opened 1.5 to 2.5 hours earlier than one-day flowers.

Patterns of daily opening and closing appear well suited to reducing the risk of poor or no pollination.

Emergence and abundance of the primary pollinators, *Diadasia rinconis* and *D. opuntiae*, varies considerably among years (Ordway 1984; Ordway 1987; Neff and Simpson 1992). As a result, pollination might be inadequate in years when the bees emerge before or after peak bloom, or when their populations are small relative to the number of flowers available (Neff and Simpson 1992). Early in the flowering season, when temperatures tend to be cooler, most *O. engelmannii* flowers open in the morning and live for two days, perhaps increasing the likelihood of pollination when the presence of pollinators is uncertain. Later in the season, when days are warmer, pollinators are more abundant. They are active throughout the day (Ordway 1984), but typically make many more flower visits in the morning than in the afternoon (Fig. 2). One-day flowers, by opening in the morning, receive frequent visitation but are also likely to be spent by the end of the day as a consequence of higher temperatures. Two-day flowers, by opening after noon on their first day, receive few visits then, but, by opening well before all other flowers on their second day, gain a virtual monopoly on early morning visitation. The main risk to this strategy is that very warm temperatures on the first day might preclude a second day of bloom.

These and other hypotheses, such as maximization of male or female fitness, require careful testing; in the meantime, it is evident that by controlling accessibility of flowers to pollinators, temperature and time of opening might have profound implications for the reproductive biology of *O. engelmannii*.

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DIVERSIFIED GERMINATION BEHAVIOR OF *PARKINSONIA*
MICROPHYLLA (FOOTHILL PALOVERDE, FABACEAE)

JANICE E. BOWERS

U.S. Geological Survey, 1675 W. Anklam Road, Tucson, AZ 85745

jebowers@usgs.gov

ABSTRACT

Diversified germination behavior has been well documented for winter annuals in the Sonoran Desert but has been reported for few woody plants in the region. Despite a long-held assumption that seeds of the leguminous tree *Parkinsonia microphylla* (foothill paloverde) are impermeable to water until scarified by natural abrasion, a variable proportion can germinate shortly after dispersal without scarification. Seed crops thus comprise nondormant as well as dormant seeds and exhibit diversified germination behavior. Under controlled conditions (25°C), germination of unscarified seed averaged 32%. Under natural rainfall regimes, germination of unscarified seed ranged from 4% to 49%. Laboratory experiments suggest that permeability of fresh seed is highest under warm temperatures and no more than a single cycle of wetting and drying. Diversified germination behavior has profound implications for population dynamics. In the case of *P. microphylla*, the mixture of dormant and nondormant seeds promotes multiple pulses of germination each summer and ensures coordination between cohort size and soil moisture levels.

RESUMEN

Diversificación en comportamiento de germinación ha sido bien documentado para anuales invernales pero poco para plantas leñosas del Desierto Sonorense. A pesar de la suposición que las semillas de *Parkinsonia microphylla* son impermeables antes de ser escarificadas, una proporción variable de semillas pueden germinar sin escarificación siguiente a dispersión. Por lo tanto la producción anual de semillas incluye semillas aletargadas y no aletargadas cuales manifiestan diversificación en comportamiento de germinación. Bajo condiciones controladas, un promedio de 32% de las semillas se germinaron a 25°C. Con un régimen natural de lluvia, se germinaron entre 4% y 48% de las semillas no escarificadas. Experimentos indican que la permeabilidad de semillas nuevas es mas alta con temperaturas cálidas y no mas que un ciclo de humedad y sequía. Diversificación en el comportamiento de germinación tiene consecuencias profundas para la dinámica de poblaciones. En el caso de *P. microphylla* la mezcla de semillas aletargadas y no aletargadas promueve múltiple pulsos de germinación cada verano y asegura la coordinación entre el tamaño del cohorte de semillas y el nivel de la humedad del suelo.

Key Words: Climatic variability, seed dormancy, seed permeability, Sonoran Desert.

Diversified germination behavior, in which seeds from a single crop display different levels of dormancy, has profound implications for population dynamics. It is well known that winter annuals in the Sonoran Desert employ this strategy (Westoby 1981; Venable and Pake 1999), but diversified germination behavior has been reported for few woody plants in the region. Here I report on diversified germination of *Parkinsonia microphylla* Torrey, a drought-deciduous, leguminous tree common in the Sonoran Desert of Arizona and northern Mexico.

Parkinsonia microphylla flowers in late April and May and disperses seed in June. Dispersal agents include scatter-hoarding sciurid (personal observation) and heteromyid (McAuliffe 1990) rodents that bury the seeds at depths of 2 to 3 cm. Dormant seeds remain in the soil and, if not destroyed by predators or pathogens, germinate over the next several years (Shreve 1951; McAuliffe 1990; Bowers 1994). Seeds germinate in response to summer (July to October) rains ≥ 17 mm (Bowers 1994). A single cycle of wetting and drying lowers germination by 50% (Poole 1958). Given

adequate summer rain, seedlings are usually plentiful (Shreve 1917; Bowers and Turner 2002). New seedlings are highly vulnerable to predation (McAuliffe 1986; Bowers and Turner 2002) and, to a lesser extent, seasonal drought (Shreve 1917; Bowers and Turner 2002).

Some Sonoran Desert ecologists have long assumed that the hard seeds of *P. microphylla* are impermeable to water and will not germinate until scarified by natural abrasion (e.g., Shreve 1951; Turner et al. 1995), an assumption based on laboratory trials in which germination required mechanical or chemical scarification. If hard seeds will not germinate without scarification, it is safe to assume that they are dormant. Germination of unscarified *P. microphylla* seed has been reported several times but not ascribed any particular importance. In one study, $< 2\%$ of unscarified seeds germinated (McAuliffe 1990); in another, high germination (88%) was inconsistently attributed to permeable seed coats or scarification of stored seed by insects (Poole 1958). Barton (1947) found that 10% of untreated seeds imbibed water (and could presumably germinate) but did not discuss this finding.

Two observations made at Tumamoc Hill, Tucson, Arizona, suggest that despite previous assumptions, *P. microphylla* seed crops might comprise dormant and nondormant seeds. First, in spring 2002, I observed that *P. microphylla* did not flower at Tumamoc Hill after severe winter drought, and there was no seed crop. Nevertheless, 40 seedlings emerged on Area A, a 557-m² plot on Tumamoc Hill, following adequate rains in July. The following winter was also very dry, and again *P. microphylla* failed to flower on Tumamoc Hill. After germinating rains in August 2003, there were 11 new seedlings on Area A. The emergence of seedlings after two years of crop failure confirms the existence of a between-year seed bank (McAuliffe 1990) and indicates that some seeds are dormant. Second, after summer rains in August 1997, I observed emergence of *P. microphylla* seedlings at a second site near Tucson, Arizona. Seedlings emerged in tight clusters as if from rodent caches (McAuliffe 1990). Because the soil had been thoroughly dug and turned the previous winter, these seeds must have been cached soon after they ripened in June 1997; if so, they were no more than two months in age at the time of germination. Evidently, a proportion of the seed crop can germinate in the year of dispersal and is nondormant.

Taken together, these observations suggest that *P. microphylla* displays diversified germination behavior. This study used germination experiments under controlled and natural conditions to confirm that seeds can indeed germinate in the year of dispersal, to determine what proportion of the seed crop is nondormant, and to learn whether this proportion changes in response to environmental factors such as temperature or cycles of wetting and drying.

METHODS

Study Sites

Observations reported above were made at the Tumamoc Hill and Ruthann Road sites; outdoor germination experiments were conducted at the Ruthann Road site. The Tumamoc Hill site is a 352-ha nature preserve and research station just west of downtown Tucson, AZ (32°13'N, 111°05'W). Elevations range from 725 to 948 m above sea level. The Ruthann Road site is just northwest of Tucson at 720 m above sea level. Although this site is in a residential area, housing density is low, and much natural vegetation has been preserved. The sites are about 11 km apart and support vegetation typical of the Arizona Upland subdivision of the Sonoran Desert (Shreve 1951). Native birds, rodents, lagomorphs, canids, and other wildlife are abundant at both sites. At Tucson, rainfall averages 280 mm per yr. Almost half comes during July, August, and September; most of the remainder falls between November and March (Sellers et al. 1985). Average maximum and minimum daily temperatures are

18.6°C and 2.4°C during January, the coldest month, and 37.9°C and 22.8°C in June, the hottest month (Sellers et al. 1985). In June and early July, daily soil temperatures at a depth of 7.5 cm commonly fluctuate between 25°C and 52°C (Shreve 1931).

Germination under Natural Conditions

Two experiments were conducted under natural conditions to confirm that *P. microphylla* seeds can indeed germinate in the year of dispersal. Ripe seeds were harvested from several trees on June 15, 2001, and divided into eight replicates of 20 seeds each. Half the replicates were scarified by rubbing the seed coats with a metal file. On June 18, 2001, a shallow trench approximately 4 cm × 100 cm × 200 cm was dug in dry desert soil. Eight cylindrical cages made of narrow-mesh (6.4 mm) hardware cloth were placed in the trench; the cages were about 14 cm high and 36 cm in diameter. Replicates were randomly assigned to cages. Seeds were placed in a single layer on the ground within each cage, then covered with soil to a depth of about 2.5 cm. The trench was backfilled so that its surface was flush with the soil in the cages. To protect seeds from animals, cages were covered with lids of hardware cloth weighted down by rocks. Germination in response to summer rains was recorded from July to September 2001.

The experiment was repeated with some modifications two years later. Ripe seeds were harvested on June 15, 2003, and divided into four replicates of 25 seeds each. A razor blade was used to nick all seeds in two replicates. Seeds were sown in desert soil in four plastic nursery flats (32.5 cm × 32.5 cm × 7.5 cm) at a depth of 2.5 cm on June 17, 2003. Flats were placed in a shallow trench in the ground, then the trench was backfilled until the soil surface was flush with the top of the flats. A wire screen was placed over the flats to protect seeds from birds and rodents. Again, germinations were recorded throughout the summer. Ungermminated seeds were retrieved at the end of the experiment and scarified with a razor blade, whether previously scarified or not. Seeds were pooled within treatments, then placed on moist filter paper in Petri dishes, sealed inside small, transparent plastic bags, and germinated at room temperature (25°C).

Germination under Controlled Conditions

Seeds used in the following experiments were harvested from trees on June 22, 2003, and stored in small lots in Petri dishes at room temperature (25°C) until use. Scarified seeds were treated by nicking the seed coat with a razor blade. All seeds were germinated or incubated on moist filter paper in Petri dishes that were individually sealed inside small, transparent plastic bags. Distilled water was added as necessary to maintain an even moisture level. During germination or incubation, seeds were

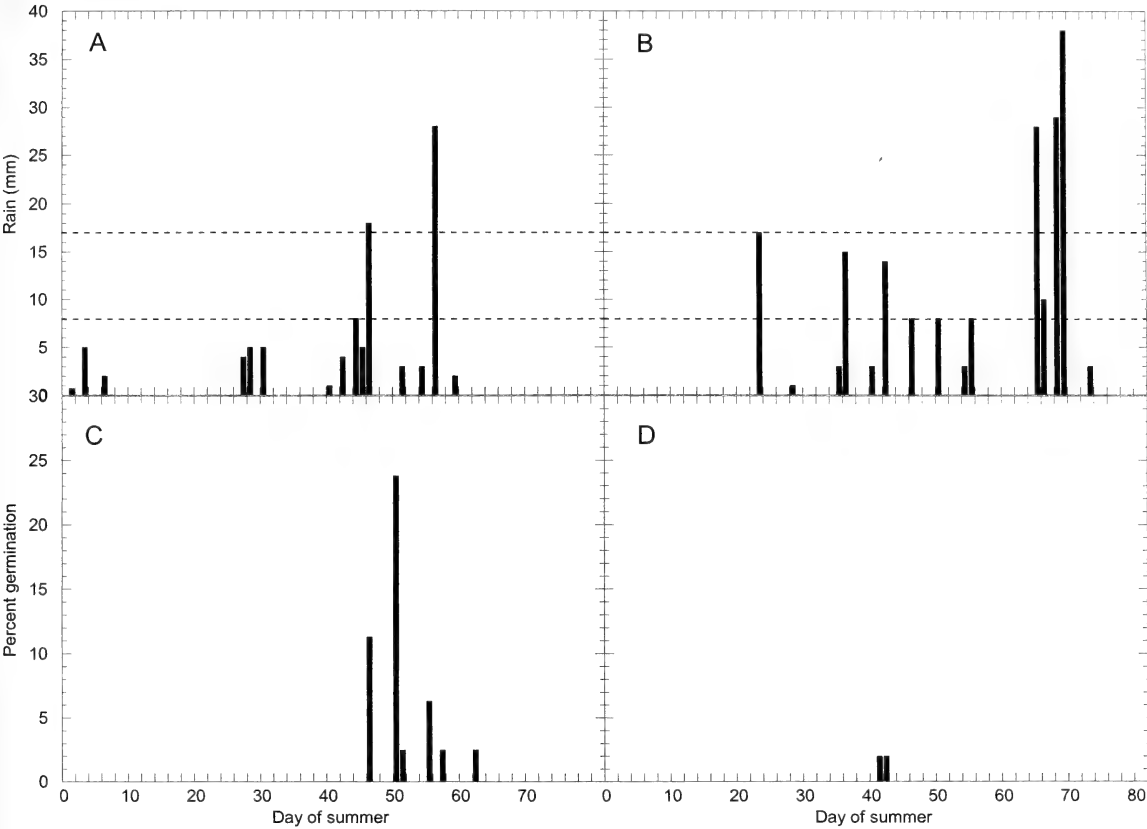


FIG. 1. Germination of unscarified *Parkinsonia microphylla* seed under natural conditions in 2001 and 2003. Scarified seeds not shown. On the X axis, days are numbered consecutively from June 20 to September 6. Dashed lines represent the 17-mm threshold for germination and the 8-mm threshold for effective precipitation at a depth of 2 to 3 cm. (A) Summer rain (mm) in 2001, Tucson, Arizona. (B) Summer rain (mm) in 2003, Tucson, Arizona. (C) Percent germination in 2001 (N = 80 seeds, replicates pooled). (D) Percent germination in 2003 (N = 50 seeds, replicates pooled).

kept at constant temperatures in an incubation chamber (40°C) or in a temperature-controlled room (25°C). Germination of *P. microphylla* is essentially indifferent to light (Poole 1958); therefore, seeds were maintained at ambient light levels, about 12 hr day/night.

To determine viability of fresh seed, scarified and unscarified seeds were germinated at 25°C in four separate trials. Seeds ranged in age from five days in the first trial to 64 d in the last. For each treatment there were two replicates of 25 seeds each. Germination was monitored for eight days.

The effect of wetting followed by drying was tested with seeds that were 75 d of age at the start of the experiment. Seeds were subjected to zero, one, three, or five cycles of wetting and drying at 25°C or 40°C. There were two replicates of 25 seeds each for every treatment. For each wetting/drying cycle, seeds were incubated in covered Petri dishes on moist filter paper at 25°C or 40°C for 24 hr, then placed in uncovered Petri dishes on dry filter paper and kept for four days at the same temperature as before. These parameters reflected moisture and temperature conditions typical of the

summer rainy season. At the end of one, three, or five wetting/drying cycles, seeds were germinated without delay at 25°C for five days. Seeds given zero wetting/drying cycles were germinated at 25°C or 40°C for five days. The short germination period approximated the brief duration of soil moisture after summer rains. Analysis of variance was used to determine the effect of number of cycles and temperature on percent germination. Before analysis, percents were arcsine-transformed to more closely approximate a normal distribution. Percent germination was calculated after adjusting sample size to correct for any seeds that germinated during the treatment phase.

RESULTS

Germination under Natural Conditions

In 2001, summer rains began in late June but no single storm was large enough to trigger germination (≥ 17 mm) until the beginning of August, when 30 mm of rain fell over three days (Fig. 1a). Emergence of unscarified seed was first observed on August 6 and continued intermittently through August

20 in response to additional storms (Fig. 1c). Mean germination for scarified and unscarified seeds was 17.5% (SD = 31.8%) and 48.7% (SD = 12.5%), respectively. The means were not significantly different in a t-test using arcsine-transformed values ($t = 1.7$, $P = 0.16$). Variables were transformed before analysis to approximate a normal distribution. The poor germination of scarified seeds was unexpected and suggested that many seeds were incompletely scarified.

In 2003, summer rains started in mid-July (Fig. 1b). The first storm reached the 17-mm threshold but did not trigger germination of unscarified seed. Some scarified seeds did germinate in response to this rain. The next substantial storm, 15 mm on July 25, triggered germination of two unscarified seedlings on July 30 and 31 (Fig. 1d); evidently the storm was not heavy enough to bring about mass germination. Successive rains were frequent but light until a rain of 28 mm on August 23. No unscarified seeds emerged in response to this storm, nor to storms totaling 67 mm on August 26 and August 27. Mean germination of scarified and unscarified seeds was 70% (SD = 8.5%) and 4% (SD = 5.7%), respectively, a significant difference ($t = 9.2$, $P = 0.018$). Ungerminated seeds retrieved at the end of the experiment were highly viable; after scarification, germination averaged 88% for previously untreated seeds and 100% for previously scarified seeds.

Germination under Laboratory Conditions

During four trials, mean germination of scarified seed ranged from 86% to 98% and of unscarified seed from 20% to 50%. The mean of means was 91.5% (SD = 5.0%) for scarified seed, 32.0% (SD = 12.4%) for unscarified seed. Because scarified seed germinated to a high percentage, it appears that most if not all seeds were viable; therefore, failure of unscarified seeds to germinate can be ascribed to dormancy rather than poor viability. During germination, unscarified seeds darkened first at the hilar end, suggesting that water entered through the micropyle, hilum, or lens. Carefully controlled experiments will be needed to determine the exact point of water entry.

Mean germination after zero, one, three, and five wetting/drying cycles was 26.0%, 24.0%, 4.0%, and 6.8% for seeds incubated at 25°C, and 51.0%, 18.5%, 10.1%, and 5.4% for seeds incubated at 40°C. In ANOVA, number of cycles had a strong effect on percent germination ($F_{(3,8)} = 42.9$, $P < 0.001$), and temperature had a modest effect ($F_{(1,8)} = 7.4$, $P = 0.026$). There was a significant interaction between number of cycles and incubation temperature ($F_{(3,8)} = 9.1$, $P = 0.006$). For seeds that did not undergo wetting and drying, germination was at 40°C was twice that at 25°C. Under either temperature regime, germination declined sharply after one wetting/drying cycle.

DISCUSSION

The results of this study demonstrate that a variable proportion of fresh *P. microphylla* seeds can germinate without scarification. Under controlled conditions, germination of unscarified seed at 25°C ranged from 20% to 34% and averaged 32% (SD = 13.4%). Under natural rainfall regimes, germination of unscarified *P. microphylla* seed showed considerable interannual variability, averaging 49% in 2001 and 4% in 2003.

Seed-coat impermeability is usually a function of lignified palisade cells in the seed coat (Baskin and Baskin 1998; Baskin et al. 2000). Many hard-seeded legumes produce some permeable seeds that can germinate without scarification; the point of water entry is often the micropyle, hilum, or lens (Korban et al. 1981; Agbo et al. 1987; Baskin et al. 2000). In the case of *P. microphylla*, permeability might depend in part on whether the hilar region is completely sealed. In the wetting/drying experiment, germination of untreated seed (zero cycles) was greater at 40°C (51%) than at 25°C (26%), suggesting that warmth influenced permeability in the hilar region. Because germination declined as number of wetting/drying cycles increased, it appeared that patterns of moisture also had a strong effect on permeability. Under natural conditions, patterns of moisture of course depend on rainfall. To moisten buried *P. microphylla* seeds, rains must penetrate to a depth of about 2 to 3 cm, the depth at which rodents bury seeds (McAuliffe 1990). On Tumamoc Hill, light rains (<8 mm) have little effect on percent soil moisture at this depth (Shreve 1914, 1934) and are probably not involved in natural wetting/drying cycles. In 2001, there was only one storm ≥ 8 mm before germinating rains fell in early August, so buried seeds experienced no more than a single cycle of wetting and drying. In 2003, there were six storms of this magnitude before germinating rains in late August and therefore six cycles of wetting and drying. Thus, in nature as well as in the laboratory, good germination of unscarified seed was associated with minimal wetting and drying, poor germination with frequent wetting and drying.

Certain other leguminous trees with hard seeds in the northern Sonoran Desert also might exhibit diversified germination behavior. In laboratory studies, 2% to 12% of seeds of *Parkinsonia florida* (Bentham ex A. Gray) S. Watson imbibed or germinated without treatment (Barton 1947; Poole 1958), indicating that a fraction of the seed crop is nondormant. Similarly, imbibition or germination of untreated *Prosopis velutina* Wootton seeds in three different studies was 6% to 7% (Glendening and Paulson 1955), 18% (Poole 1958), and 30% (Barton 1947). Well before diversified germination behavior became a topic of interest to ecological theorists, Glendening and Paulson (1955) noted that because *Prosopis* seed coats vary in permeability,

germination of a cohort likely would be staggered. Under natural conditions, germination behavior of *Prosopis* is further complicated by the hard, leathery pericarp that surrounds the seeds. The pericarp is impermeable to water, preventing germination until it is fractured or split (Glendening and Paulson 1955), a service frequently performed in the wild by heteromyid rodents, especially *Dipodomys* (Cox et al. 1993). The strategy of *Olneya tesota* A. Gray apparently differs somewhat from that of *Parkinsonia* and *Prosopis*. When dispersed in June, *Olneya* seeds are soft and highly germinable (77%) (Poole 1958; see also Shreve 1951), but they require scarification when aged (Went 1957; Emery 1988). The increase in seed-coat hardness with age suggests that timely summer rains should trigger mass germination soon after dispersal, but, if summer rains fail, uneaten seeds should gradually harden, facilitating persistence until the following summer. Further studies are needed to determine whether these species do indeed exhibit diversified germination behavior.

One consequence of diversified germination behavior for *P. microphylla* is multiple pulses of germination and emergence each summer (Bowers 1994; Bowers and Turner 2002). The first pulse might well represent nondormant seeds dispersed earlier that summer; later pulses might comprise older seeds newly released from dormancy. The factors that break dormancy in this species are unknown but as for many other hard-seeded legumes might involve exposure to high or widely fluctuating temperatures (Baskin and Baskin 1998). By distributing risk through time, multiple emergence pulses might increase the probability of establishment. The primary risk is probably predation; the limited data available suggest that most *P. microphylla* seedlings are eaten before they have a chance to die of drought stress (McAuliffe 1986; Bowers and Turner 2002). Another consequence of diversified germination behavior is that, as for winter annuals, the proportion of seeds that germinate varies between years and depends at least in part on environmental factors. Given heavy rain soon after dispersal, seeds germinate to a relatively high percentage. If summer rains are frequent and light, only a small percentage of the seed crop remains nondormant. Thus, cohorts derived from fresh seed are likely to be large when moisture is ample, small when moisture is barely adequate. By ensuring coordination between cohort size and soil moisture, responsiveness to wetting/drying cycles should be an effective strategy for dealing with interannual and spatial climatic variability in the Sonoran Desert. Future investigations could examine the possibility that diversified germination behavior in *P. microphylla* functions as a bet-hedging strategy in which reduction in the fitness of individual generations results in increased fitness over many generations.

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ASPECTS OF REPRODUCTIVE BIOLOGY IN THE SEXUALLY DIMORPHIC SHRUB *MALOSMA LAURINA* (ANACARDIACEAE)

GARY B. PERLMUTTER¹

240 N. Alvarado Avenue, Ojai, CA 93023

ABSTRACT

Gender distributions of the dimorphic shrub *Malosma laurina* were studied in a population in Ventura County, California, via assessment of population sex ratio, estimation of phenotypic and functional gender, and analysis of sex expression of individual plants. Reproductive investment was investigated via flower number and biomass as well as its effects on phenology and vegetative growth. The population studied had 30% female shrubs, which departed from a 1:1 ratio by Chi square analysis. Both phenotypic and functional gender measurements of males were less than 2% female, demonstrating *M. laurina* to be functionally dioecious. Varying fruit production was found both among and within male shrubs over three successive seasons, without apparent causal relationships with other factors. Reproductive investment was found to be similar between sex morphs at the individual level, despite heavier flower buds among males. Phenologies of thyrsi (i.e., inflorescences) were synchronous between the sex morphs in both flower and fruit development. Vegetative characters (i.e., branch internodal length and leaf measurements) did not differ between the morphs. These results suggest that the near complete dioecy of *M. laurina* appears to have evolved along the gynodioecy pathway from hermaphroditism toward dioecy.

Key Words: Anacardiaceae, biomass, gender distributions, gynodioecy pathway, *Malosma laurina*, phenology, reproductive investment.

The phenomenon of dimorphic breeding systems in plants has been a subject of considerable interest since the time of Darwin's work, *The Different Forms of Flowers on Plants of the Same Species* (1877). This interest has spurred the compilations of texts by Richards (1986), Lovett Doust and Lovett Doust (1988), and Geber et al. (1999). In addition, many selection models have been offered to propose evolutionary pathways toward dioecy with a variety of factors being selected for (Charnov and Bull 1977; Charlesworth and Charlesworth 1978; Beach 1981; Charnov et al. 1981; Ross 1982; Freeman et al. 1997; Charlesworth 1999; Delph et al. 1999; Geber 1999; Marshall and Ganders 2001). Empirically, a variety of dimorphic conditions have been described in many unrelated taxa around the globe (reviewed by Sakai and Weller 1999). Because of this variety of breeding system evolution among seed plants, Baker (1984) had emphasized the need to examine each case individually. Incidentally, several reports of case studies have appeared in the literature in recent years (e.g., Delph et al. 1999; Bram and Quinn 2000; Olson and Antonovics 2000; Marshall and Ganders 2001; Strittmatter et al. 2002), which help to elucidate the evolutionary histories of the species examined.

One such species that deserves study is *Malosma laurina* (Nutt.) Abrams (laurel sumac, Anacardiaceae), in which the sex morphs have only recently been described as female, male, and andromonoecious (Perlmutter 1998). While the breeding system

of *M. laurina* has been classified as "polygamo-dioecious" (Barkley 1937; Perlmutter 1998), this may not be the most accurate term. Depending on author, the breeding system comprising of females, which are constant in their sex expression and hermaphrodites exhibiting reduced and varying female expression can also be termed "gynodioecious" (Lloyd 1973, 1980; Webb 1979; Wolfe and Schmida 1997) or "subdioecious" (Delph 1990; Sakai and Weller 1999). In this paper such classification is not used, in recognition of the variability of sex expression among andromonoecious individuals that can affect the appearance of a population's composition.

Given the continuity of breeding systems from monomorphic to dimorphic states across species in general (Lloyd 1980; Sakai and Weller 1999) and the variation in female expression among andromonoecious individuals of *M. laurina* in particular (Perlmutter 1998), gender quantification through phenotypic and functional gender estimates can yield a more accurate description of *M. laurina*'s breeding system along the gradient between hermaphroditism and dioecy. Further, while variation of gender expression has been only generally estimated previously (Perlmutter 1998), no quantitative analysis has been conducted to explore causal relationships, such as sex allocation trade-offs within hermaphrodites (Wolfe and Schmida 1997; Geber 1999; Olson and Antonovics 2000) or environmental influence (Lloyd and Bawa 1984) for this species.

This report directly follows my earlier paper (Perlmutter 1998), which describes the sex morphs of *M. laurina*. The objectives of the present study

¹ Current address: 7025 Mine Creek Lane, Raleigh, NC 27615. e-mail: lushik@aol.com

were to further investigate how the sex morphs differ from each other and to quantify the variation of female expression both among andromonoecious sumacs and within these individuals over successive reproductive bouts (i.e., their gender distribution). The findings of this study also aim to more accurately describe this species' breeding system in context with evolutionary models. Areas of *M. laurina* reproductive biology examined include: population sex ratio, phenology, reproductive investment, vegetative dimorphism, phenotypic and functional gender estimates, and variation of sex expression among andromonoecious plants.

During the course of the study certain plants originally designated "male" were later found to produce fruit and others termed "andromonoecious" based on floral characteristics never fruited. Following the convention of Lloyd (1973, 1974, 1980; Lloyd and Webb 1977; Hoffmann and Aliende 1984; Delph 1990) the andromonoecious and male sex morphs are here treated together as "male", in recognition of their polleniferous function.

MATERIALS AND METHODS

Study Species

Malosma laurina is a large 2–4 m tall evergreen shrub found on sunny slopes and canyons in coastal sage scrub and chaparral plant communities of southern California, and Baja California, Mexico at elevations 0–1000 m (Munz 1974; Wilken 1993). The genus is monotypic, except for the fossil *M. prelaurina* found in Miocene and Pliocene deposits of southern California (Axelrod 1937, 1950). Flowers of *M. laurina* are small (1 mm), white and borne on dense inflorescences (hereafter "thyrsi" following Barkley [1937]), numbering up to 5600 per thyrsus (personal observation). Laurel sumac is bee-pollinated, producing drupes that dry after ripening and often persist in the canopy for at least one year (personal observation). This species is sexually dimorphic with female shrubs exhibiting flowers with stunted androecia exclusively (Engler 1883; Perlmutter 1998) and male plants having thyrsi with approximately 0–25% perfect flowers among those with reduced gynoeceia, which produce an estimated 0–25% fruit per plant (Perlmutter 1998).

Study Site

The laurel sumac population studied lay on a south-facing slope along the Cozy Dell Trail, 2 km from the trailhead at Hwy 33 in the Los Padres National Forest, 4 km NW of Ojai, Ventura County, California, (34°27'N, 119°16'W). Located 22 km from the coast, this area is in the Transition Climate Zone (Bailey 1966), influenced by a mixture of maritime and continental air masses (Hickman 1993). Mean climate data for Ojai from 1961–1990

include annual rainfall of 52.6 cm plus January minimum and August maximum temperatures of 2.6 and 32.2°C, respectively (NOAA 1992). At 460 m elevation the site lay in a mosaic chaparral dominated by *Salvia mellifera* Greene, *S. leucophylla* Greene, *M. laurina*, *Eriogonum fasciculatum* (Benth.) Torr. & A. Gray, *Ceanothus spinosus* Nutt. and *Artemisia californica* Less. Due to the difficulty of navigating through dense chaparral on steep terrain, thirty shrubs were selected for study along the trail and an adjoining firebreak.

Phenology

Beginning May 2001 I tracked the phenology of the 30 shrubs from their initial budding through the end of each individual's reproductive cycle, here defined as when all flowers and/or fruits had dried. Visits were made weekly, recording the phenological stages of thyrsi of each shrub, which were classified into five stages: growing buds, mature buds, open flowers, developing fruits and ripe fruits. Since sumacs have numerous thyrsi per individual, which do not necessarily develop synchronously, I recorded all phenological stages observed per shrub during each visit to better represent each sumac's phenology. Phenograms were produced for each stage and were compared between the morphs. Onset and peak dates of each stage plus flower and fruit development periods were determined and compared. Flower development period (D_{Fi}) is here defined as the number of weeks from the date when buds were first observed to the date when at least 50% of a population is in flower (after Bowers [1996]). Similarly, fruit development period (D_{Fi}) is the number of weeks from first observation of developing fruits until when at least 50% have ripened but not dried.

Sex Ratio

Each sumac was sexed upon selection prior to the 2001 reproductive season by checking for abundant dried fruits from the previous season. Those plants laden with fruits were classified female, and those with few or none were classified male. Considering the small sample size under study ($n = 30$), 26 additional shrubs were sexed in 2002 for a larger population of 56. This larger sample's sex ratio was tested against a 1:1 ratio by Chi square.

Inflorescence Measurements

Just before flowering, one representative (i.e., of average size) thyrsus in the mature bud stage was collected from each study plant, and the following measurements were taken: length, width, fresh weight, and number of buds. The timing of harvest was aimed to minimize loss of fragile flowers or floral parts during handling, which could affect accuracy of measurements. Weights in the field were taken with a Pesola 3 g (Pesola, Switzerland) spring scale. Upon immediate return from the field, 2–4

buds of each collected thyrus were removed and fresh-weighed using a Sartorius GMBH analytical balance (Sartorius, Göttingen, Germany). Although dried weights would be preferred, equipment was not available to obtain consistent dry mass, thus leaving a less accurate measure as an approximation of biomass. I pooled these weights per morph ($n_f = 24$, $n_m = 62$) for comparison testing. Thyrsi were collected and processed again in the same manner when fruits had ripened. In October 2002 I collected and weighed five seeds from one 2001-season thyrus, dried on the canopies of eight females and four males, for further comparison between the two morphs. Means of all variables were tested for sex morph differences by two-tailed Student's *t*-test.

Reproductive Investment Estimates

I estimated total reproductive biomass invested by each sex morph at the individual level by multiplying the mean budding thyrus weight (pooled from the individual weights collected in the field) by the mean number of thyrsi per shrub (i.e., its thyrus load). Similarly, I estimated the reproductive investment in terms of flowers produced per plant. To calculate a plant's thyrus load, photographs of each sumac were taken when in bloom and thyrsi were counted photometrically, since a physical count of numerous thyrsi on a given canopy of these large shrubs would risk count replication. All visible thyrsi were counted on each photograph to represent one shrub face, then doubled to estimate that of the whole plant. This method assumes even inflorescence distribution over the entire plant canopy as based on previous examinations of other sumacs (personal observation) and does not take into account possible uneven distribution resulting from localized canopy disturbance on the hinter side. Because the hinter side of a given sumac is not always accessible due to the dense chaparral vegetation and/or topography, this method only gives a rough estimate of the plant's true thyrus load.

Phenotypic and Functional Gender Estimates

The phenotypic gender of males is expressed as the proportion of flowers producing fruit, which was calculated from the above shrub flower and fruit numbers estimated in the following manner. On each male-fertile plant the number of fruiting thyrsi was counted in a sample of 20 thyrsi. The proportion of fruiting thyrsi was multiplied by the pooled mean number of counted fruits per sampled thyrus and multiplied again by the estimated number of thyrsi per shrub (see above). A gender plot was generated from these data to illustrate their distribution.

An estimate of functional gender of each plant, expressed as its relative femaleness (G_f), was calculated using a pair of formulae developed by

Lloyd (1980) and used by himself and subsequent workers (Barrett 1992; Maurice et al. 1998; Ramsey and Vaughton 2001):

$$G_i = d_i / (d_i + l_i E)$$

and

$$E = \sum d_i / \sum l_i$$

where d_i is the number of ovules (i.e., fruits) produced by plant i and l_i is the number of polleniferous flowers produced by plant i . An assumption to this calculation is that each polleniferous flower has equal probability to contribute to the next generation as each ovuliferous flower in the population, hence the equivalence factor E of the second equation being a ratio of the two sex functions for the population. Using the estimated flower and fruiting loads of each plant, G_i was calculated for each shrub and averaged for the sample population of males (G_m). The functional gender of females (G_f), which were constant in their sex expression, was 1.0, representing both the individual and population levels.

Male Inconstancy

In addition to the 2001 fruiting assessment (i.e., proportion fruits per flower load as estimated for the above phenotypic gender estimates) of each male, I had recorded assessments of the dried 2000 fruit crop in 2001 and the next year's crop in 2002 to check for temporal changes in sex expression. The three sets of proportion data were arcsine-transformed to normalize for comparison testing (Zar 1984). Single-factor ANOVA was performed on the transformed data sets to test for differences by year.

Vegetative Dimorphism

To determine if the sex morphs differed in vegetative growth, I took two internodal lengths (the distance between the current season's thyrus and the previous year's, thus representing one year's growth) of each plant in 2001. These data were averaged per individual, and I analyzed the averages by sex morph using Student's *t*-test (two-tailed). In 2002 I measured the length and width of two leaves per plant and similarly tested per sex morph.

Statistical analyses were performed using Excel 2000 (Microsoft 1999) with consultation of Zar (1984). As the data sets were not consistently normal in distribution nor consistently homoscedastic, robust tests were chosen for analysis (i.e., two-tailed Student's *t*-tests and single-factor ANOVA) (Zar 1984). The level of significance for all statistical tests was set *a priori* at 0.05.

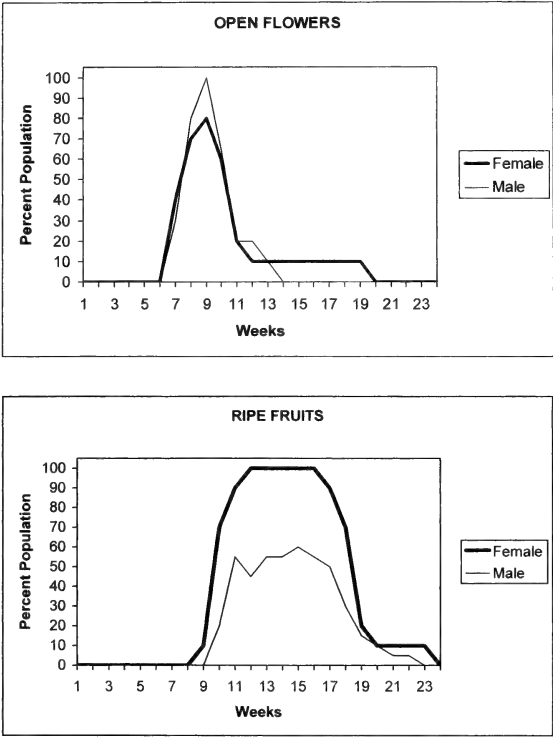


FIG. 1. Phenograms of open flower and ripe fruit stages of male and female *Malosma laurina* shrubs at Cozy Dell Trail, Ventura County, California, 2001. Week 1 began on 6 May.

RESULTS

Phenology

The reproductive season, here defined as from the first emergence of buds to the drying of all fruits, lasted 24 wks, from 6 May through 14 October 2001. Onset and peak dates for all stages measured were synchronous between the sex morphs, differing at most by one week. Flowering began on 17 June and peaked on 1 July (Fig. 1) with D_{Fi} = 7 wk for both sex morphs. Fruits began to develop immediately after flowering and were at peak ripeness from mid-July to mid-August (Fig. 1); female D_{Fr} = 2 wks and male D_{Fr} = 3 wks. Post-peak phenology was less uniform, which resulted from certain plants delaying part of their reproductive efforts due to recovery from localized

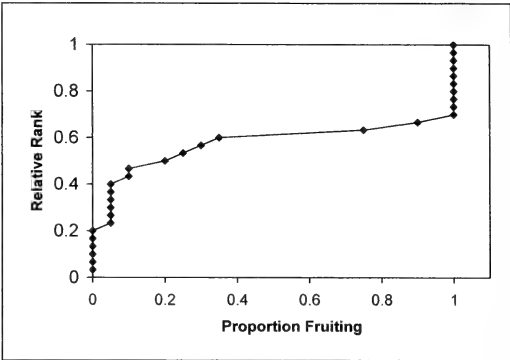


FIG. 2. Distributions of phenotypic gender in males and females of *Malosma laurina* (n = 30) in the 2001 reproductive season.

canopy damage, possibly from disease (personal observation).

Sex Ratio

The sex ratio measured in 2002 measured 17:39 female:male plants, or 30% females (n = 56). This ratio tested to depart from a 1:1 by Chi square (χ^2 = 8.64, df = 1, $P < 0.005$), suggesting a deficiency of females.

Phenotypic and Functional Gender

Six of the 20 male sumacs did not produce any fruit in 2001; among the remaining 14 shrubs proportion of fruiting thyrsi varied from 5–90% (Fig. 2). Altogether, the phenotypic gender was calculated to be 8.0×10^{-5} , or an estimated 0.008% of the flowers on the males produced fruit in 2001. Functionally, males produced 97.47% fewer fruit than females on average (Table 1), which is also reflected in the number of fruits per thyrsus (Table 2). The average G_{δ} = 0.011 for the sample population in 2001, meaning that as a population males contributed only 1.1% of their genes via ovules to the next generation.

Male Inconstancy

Of the 20 male sumacs studied ten produced fruits in 2000, fourteen fruited in 2001 and ten fruited in 2002, with four plants not producing any fruit during the three-year period. As a population

TABLE 1. ESTIMATED REPRODUCTIVE PERFORMANCE OF MALE AND FEMALE SHRUBS OF *MALOSMA LAURINA* AT COZY DELL TRAIL, VENTURA COUNTY, CALIFORNIA, 2001. Numbers in parentheses are one standard deviation.

| | Male plants | Female plants |
|---------------------------------------|------------------|----------------|
| Number plants (a) | 20 | 10 |
| Average no. thyrsi per plant (b) | 445.2 (±331.9) | 703.7 (±535.9) |
| Average no. flowers per thyrsus (c) | 1492.7 (±1294.5) | 937.2 (±761.4) |
| Average no. flowers per plant (b × c) | 664 624.7 | 659 507.6 |
| Average no. fruit per plant (d) | 1118.8 | 529 265.4 |

TABLE 2. THYRSUS MEAN (\pm SD) DATA AND STUDENT'S T-TEST (TWO-TAILED) RESULTS BETWEEN TEN FEMALE AND TWENTY MALE SHRUBS OF *M. LAURINA* AT COZY DELL TRAIL, VENTURA COUNTY, CALIFORNIA 2001. ^a Not calculated due to influence of dried flowers and drying stalks. * $P < 0.05$, *** $P < 0.001$.

| Variable | Female | Male | Student's <i>t</i> |
|-----------------------------|--------------------|---------------------|--------------------|
| Budding thyrsus weight (g) | 3.03 (\pm 1.47) | 4.70 (\pm 3.32) | 1.44 |
| Fresh bud mass (mg) | 0.92 (\pm 0.26) | 1.86 (\pm 0.80) | 4.12*** |
| Fruiting thyrsus weight (g) | 9.08 (\pm 4.28) | — ^a | — ^a |
| No. fruits per thyrsus | 608 (\pm 295) | 10.5 (\pm 17.4) | 8.77*** |
| Fresh fruit mass (mg) | 8.59 (\pm 1.49) | 11.68 (\pm 3.50) | 2.50* |
| Dry seed mass (mg) | 2.18 (\pm 0.53) | 2.85 (\pm 1.04) | 1.21 |

the males did not significantly differ in fruiting from 2000–2002 (single-factor ANOVA, $F = 2.72$, $P = 0.07$). Individual shrubs, however, varied in the amount of fruiting among years in a seemingly random fashion.

Reproductive Investment

Male and female sumacs produced similar numbers of flowers per shrub (Table 1) with similar reproductive biomass investments (i.e., total inflorescence weights) of 2.09 kg and 2.13 kg, respectively. While both morphs produced similar numbers of similarly heavy thyrsi, the mean bud weight from females was half that from males (Table 2). Average fruit weight among male plants was 1.5 times greater than among females. Dry seed weights of males were slightly greater than those of females.

Vegetative Characters

Mean (\pm SD) internodal lengths of the two morphs were 10.1 (\pm 4.1) and 11.8 (\pm 6.8) cm for the female and male plants, respectively. Leaf lengths and widths for female sumacs were 6.5 (\pm 1.1) and 2.9 (\pm 0.4) cm, while those for males were 5.7 (\pm 0.8) and 2.6 (\pm 0.4) cm, respectively. None of these variables differed significantly, although leaves of females were nearly wider (Student's $t = 2.16$, $P = 0.05$).

DISCUSSION

In this study the sex morphs of *Malosma laurina* were found to have synchronous reproductive phenologies and similar vegetative characters. Differences detected include a male-biased sex ratio, plus males having heavier flowers (inferred by bud mass), and far fewer, yet heavier fruits. While not significant, male inflorescences were slightly larger and had more flowers, plus the few seeds that did develop on these plants were slightly heavier than those of females. The gender distributions of the sex morphs revealed *M. laurina* to be functionally dioecious with a very low female expression by male plants. Although this study is from a single population, the patterns observed in Matilija Canyon (Perlmutter 1998), located 9.5 km WNW from the study site, and data from other sites (see below)

support the findings here and together are suggestive for the species.

Phenology

Flowering synchrony between the sex morphs is consistent with other populations in Ventura County (personal observation), but fruiting synchrony appears to be unique to the Cozy Dell population. In Matilija Canyon males fruited 3 wk later (Perlmutter 1998) and in the Santa Monica Mountains (a coastal site in Ventura County near Point Mugu, California) they fruited up to 7 wk later than females (personal observation). Synchronous flowering has been argued to maximize pollination efficiency through poorly selective insects (Hoffmann and Allende 1984) such as bees and flies. Although not quantified in this study, pollinators observed visiting shrubs include European honeybees (*Apis mellifera*) plus occasional native bumble bees (*Bombus* sp.), and hover flies (Diptera: Syrphidae). The differential fruiting phenology found in the three populations could be related to local environmental conditions. Further study is needed.

Sex Ratio

The population studied showed to be 30 percent female. In five populations examined across Santa Barbara, Ventura and Los Angeles counties ($n_i = 19$ –22) in 1996, most also had low female frequencies, ranging 21–58%. Two of these populations tested significant from a 1:1 ratio. While these results suggest a variable pattern of reduced female frequency among laurel sumac populations, caution should be taken in the interpretation of these data due to the small sample sizes. Study of larger populations ($n_i > 100$) is encouraged to confirm this pattern and investigate potential causes.

Gender Estimates

The phenotypic and functional gender results indicate that the *M. laurina* population at the Cozy Dell Trail is functionally dioecious. Populations examined in 1996 ranged 13–63% fruiting among males (i.e., incidence of fruiting per individual), within which the population of the current study lies at 30% at the individual level. Arroyo and Ra-

ven (1975) similarly found near dioecy in two morphologically gynodioecious *Fuchsia* species; less than 10% of hermaphrodites in each species produced fruit, concluding them to be "functionally subdioecious." Lloyd (1980) in his pioneering study using the gender quantification formulae revealed the dimorphic umbel *Gingidia montana* to have phenotypic gender estimates of males to range from 0–92.7% fruiting per individual, and 33.7% fruiting for all males pooled, which is very similar to the this study's results. Functional genders for the female and "male" were $G_{\phi} = 1.0$ and average $G_{\delta} = 0.23$, respectively. Although more hermaphroditic than *M. laurina* in this study, Lloyd concluded that *G. montana* represents an intermediate stage in the gynodioecy pathway (a theoretical evolutionary pathway from hermaphroditism to dioecy as postulated by Charlesworth and Charlesworth [1978]), with males placed on "average about halfway between equal transmission via pollen and ovules (i.e., hermaphroditism) and strict unisexuality." Barrett (1992), who also used Lloyd's formulae, found even greater variation in gender estimates among populations of the Australian geophyte *Wurmbea dioica*. In three populations of *W. dioica* average G_{ϕ} values ranged from 0.27–0.32 (Ramsey and Vaughton 2001). In comparison with the above case studies this study's findings suggest that the breeding system in *M. laurina* likewise demonstrates the gynodioecy pathway.

Male Inconstancy

No pattern of female expression among males was found in the Cozy Dell population, suggesting this to be nonadaptive developmental noise as described by Lloyd and Bawa (1984). An alternate explanation is differential pollination among individuals, but as bees were observed at all plants regardless of sex expression, this seems unlikely. A lack of sex changing in response to factors such as age or environment is a prediction of the gynodioecy pathway (Freeman et al. 1997), further suggesting *Malosma* to demonstrate this pathway.

Reproductive Investment

The equivalent investments by the morphs in this study could be unique to the Cozy Dell population, as affected by the lack of gender dimorphism found among these plants at the inflorescence level. Flowering thyrsi pooled from six populations ($n_i = 20$) sampled in 1995–1996 across Santa Barbara, Ventura and Los Angeles counties tested longer (6.8 [± 1.3 SD] vs. 5.2 [± 1.4 SD] cm, $t = 4.79$, $P < 0.001$) and wider (9.7 [± 2.2 SD] vs. 7.8 [± 2.3 SD] cm, $t = 2.99$, $P < 0.001$) on average for the polleniferous morph, which agree with the pattern I had reported for the Matilija Canyon population (Perlmutter 1998). Therefore, males generally made a greater reproductive investment in flower number, although this is not always the case.

Biomass patterns reported here is consistent with that of other dimorphic species (Arroyo and Raven 1975; Kohn 1989; Delph 1990; Barrett 1992; Gehring and Linhart 1993; Hemborg and Karlsson 1999). However, caution should be used in the interpretation of this study's results as biomass obtained from fresh weights may only approximate the differences between morphs due to the influence of potential water content variation. Further, currencies not examined (i.e., nutrient allocation) could yield a more complete view of resource allocation than biomass alone (Hemborg and Karlsson 1999).

The greater weight of fruits from males was unexpected, yet consistent with dry seed weights, although the latter was not significant. The greater fruit dimorphism could indicate that more resources were allocated toward fruit tissues among males. A similar pattern is reported for the buffalo gourd, *Cucurbita foetidissima* (Kohn 1989) and a slight trend was observed in seeds of *Wurmbea dioica* populations (Ramsey and Vaughton 2001), although no explanation is offered in either case. Further research is needed to explore potential causes to this pattern.

Vegetative Characters

Branch apical growth and leaf sizes did not differ between females and males, which is not surprising given that reproductive investments of the two morphs were also found to be similar. Differences in life history traits, such as growth, are predicted when one sex invests more than the other toward reproduction (Delph 1999), and many reports have documented dimorphism in these traits (reviewed in Lloyd and Webb 1977). Determination of vegetative dimorphism is encouraged in populations exhibiting greater gender dimorphism (i.e., differential flower loads implied by different inflorescence sizes).

CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

In conclusion the sex ratios and gender estimates determined in this study suggest that *Malosma laurina* follows the gynodioecy pathway when compared to patterns reported in other species concluded to demonstrate this pathway. Sexual specialization in this species is nearly complete, with observable gender dimorphism, yet does not seem to extend to vegetative dimorphism, implying that resources are not a limiting factor. While the findings of this study lend insight into the reproductive biology of *M. laurina*, further investigation involving more numerous and larger-sized population samples throughout its range, as well as crossing experiments and seed fertility determinations between the morphs, could confirm and elaborate on the evolution and maintenance of this species' functionally dioecious breeding system.

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COMPENSATORY FOLIAGE GROWTH RESPONSE TO PARTIAL
DEFOLIATION IN THE DESERT PERENNIAL SHRUB
ENCELIA FARINOSA (ASTERACEAE)

DARREN R. SANDQUIST

Department of Biological Science, California State University,
Fullerton, CA 92834
dsandquist@fullerton.edu

ABSTRACT

Seasonal changes of water potential, leaf pubescence and foliage area were compared between two groups of *Encelia farinosa* (brittlebush) growing under field conditions: one group was partial defoliated, the other was left in tact. Partial defoliation at the start of seasonal drought induced compensatory foliage growth with no evidence of ecophysiological compensation, including the expected departure from leaf pubescence values of control plants. The compensatory foliage growth occurred within the first month of drought, but allocation to these additional leaves did not appear to have a pronounced effect on overall plant growth for the season. Leaf pubescence is crucial for maintaining favorable energy and water balance in this species, and it is suggested that the lack of physiological compensation may result from constraints imposed by this character, particularly its important interaction with plant water status during the hot and arid growing season in the Mojave Desert.

Key Words: Drought, leaf pubescence, physiological compensation, foliage area, herbivory.

Productivity for the desert perennial shrub *Encelia farinosa* A. Gray (brittlebush) has been shown to depend on a close coupling between seasonal changes of water availability and leaf morphology (Cunningham and Strain 1969; Odensing et al. 1974; Smith and Nobel 1977, 1978; Ehleringer and Mooney 1978; Ehleringer 1988). In particular, lower water potentials that occur during drought cause the production of new leaves with highly reflective leaf pubescence. This pubescence decreases absorption of solar radiation and helps maintain leaf temperatures within a favorable range for photosynthesis while also lowering demand for water used in transpirational cooling (Smith and Nobel 1977; Ehleringer and Mooney 1978; Ehleringer 1983). In the absence of water deficit, or when drought is ameliorated, each new leaf cohort produced develops approximately the same amount of leaf pubescence as the previous leaves rather than becoming more pubescent; however, they do not become less pubescent (Ehleringer 1982). Increasing pubescence during drought is not only beneficial on a short-term physiological basis, it is also associated with longer seasonal activity (Sandquist and Ehleringer 1997).

Although the interrelatedness of leaf pubescence development and plant water status has been extensively examined from a mechanistic standpoint in *E. farinosa*, few studies have explored the ecological factors (other than rainfall) that might affect changing water status and the consequences of these changes, including how such changes interact with constraint or plasticity of the water-relations/leaf-morphology association. For example, the response to partial defoliation, often observed for *E. farinosa*

due to herbivory (especially by rabbits) when availability of other vegetation is scarce (personal observation) or to leaf death caused by short-term freezing temperatures (Bowers 1991; Webb and Bowers 1993; Sandquist and Ehleringer 1996), might lead to lowered water demand owing to a lower transpirational surface area (foliage area; McNaughton 1979). With this, whole plant water status would not be expected to decrease at the same rate as a plant that had not been defoliated. This scenario could lead to a disruption of the usual environmental responses exhibited by *E. farinosa* during drought, especially with regard to leaf pubescence. That is, with improved plant water status leaf pubescence would not develop to the same extent as for an intact plant. Although this result might be beneficial in terms of increased leaf-level photosynthesis through higher light absorption or other physiological compensation, it could be equally detrimental owing to higher, potentially lethal, leaf temperatures, or lower water use efficiency owing to greater transpiration needed to offset higher leaf temperatures. In the latter case the relative loss of water versus carbon gain would be expected to prematurely terminate plant seasonal activity.

Defoliation also begets an imbalance of resource supply and demand between roots and shoots. With severe foliage losses, canopy resource demand becomes lower than the potential root supply. Conversely, root carbohydrate demand significantly outweighs leaf photosynthate supply. This imbalance would likely result in root die-off if there were no compensatory leaf productivity response. One alternative response to leaf defoliation might be increased allocation to new leaves rather than ramp-

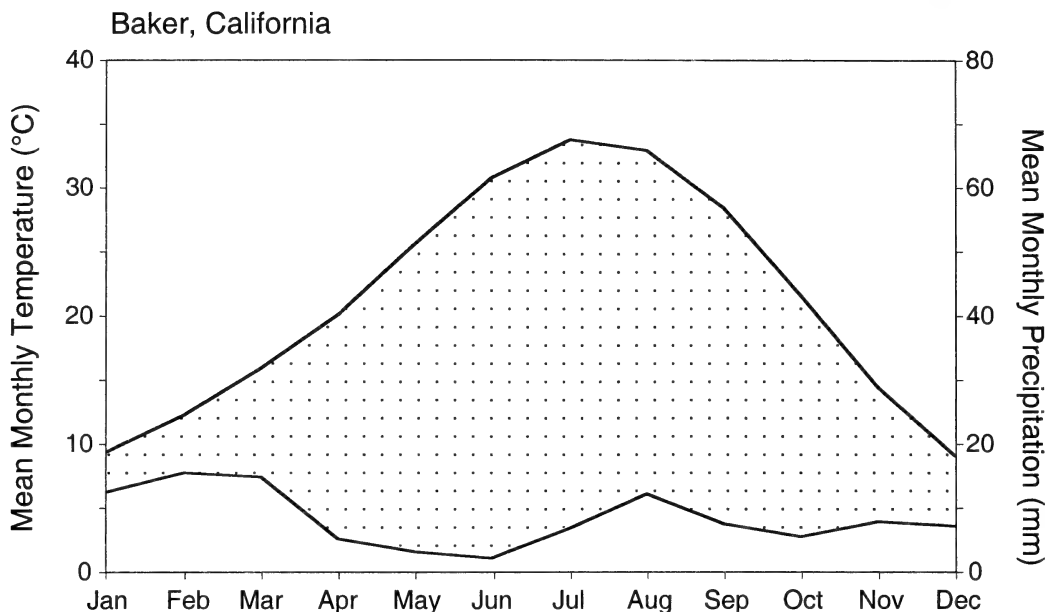


FIG. 1. Climate diagram of monthly mean temperatures (upper line) and precipitation (lower line) for Baker, California (17 km south of study site). Stippled area represents periods of relative drought. Data based on U.S. National Weather Service records for 1972 through 2002.

ing up photosynthesis of existing leaves. In addition to rectifying the imbalance of aboveground vs. belowground supply and demand, this would also re-establish a pattern of water use similar to plants that did not experience defoliation. Such allocation, however, may carry longer-term consequences in terms of reproduction, growth or storage.

In this study it was hypothesized that the reduction of transpiration area (leaves), through defoliation of *E. farinosa*, would lead to either (a) higher plant water status, and subsequently, reduced production of pubescence on new leaves, or (b) compensatory foliage production after defoliation with no changes in leaf pubescence or water status.

Identifying which responses occur owing to defoliation will provide a better understanding of plasticity and constraints associated with foliage growth and leaf pubescence development, and how these responses couple with environmental stresses such as changing water availability and herbivory.

METHODS

Study Site

The field site (35°24'48"N, 116°03'48"W) was located in the Mojave Desert approximately 17 km N of Baker, California at an elevation of 540 m. Mean annual rainfall at Baker, CA is 102 mm, and mean annual temperature is 21.3°C (Fig. 1). The population studied was located on rocky, south-facing slope where *E. farinosa* was the dominant shrub.

Measurements at the field site were made in March, April, June and July of 2001. The first measurements began two weeks after the last rainfall

of spring and ended three days prior to any summer rainfall, thereby encompassing the entire drought season of 2001. Winter and spring rainfall preceding measurements totaled 98 mm, of which 90 mm came between January 8th and March 5th. Plants were in full leaf at the time of first measurements and partial defoliation treatment (25 March).

Partial Defoliation Treatment

From within a population of 72 tagged *E. farinosa* plants, twenty mature plants with full canopies were randomly chosen for partial defoliation treatment. Twenty additional plants were randomly chosen to be controls. On 25 March 2001, after a recent period of high growth, an estimated 50% of all leaves were removed from all stems of the treatment plants. Leaves were removed from the proximal portion of each stem, leaving the upper plant canopy in tact.

Productivity and Physiological Measurement

Foliage area was estimated for all 40 plants on four dates (24 March, 28 April, 6 June and 3 July, 2001) using the following empirically derived formula (Sandquist and Ehleringer 1997),

Foliage area (m²)

$$= \frac{S}{9 \times 10^4} \times \sum_{i=1}^3 \left\{ L_i \times \left[\left(0.106 \times \sum_{j=1}^3 w_{ij} \right) + \left(0.006 \times \sum_{j=1}^3 w_{ij}^2 \right) \right] \right\}$$

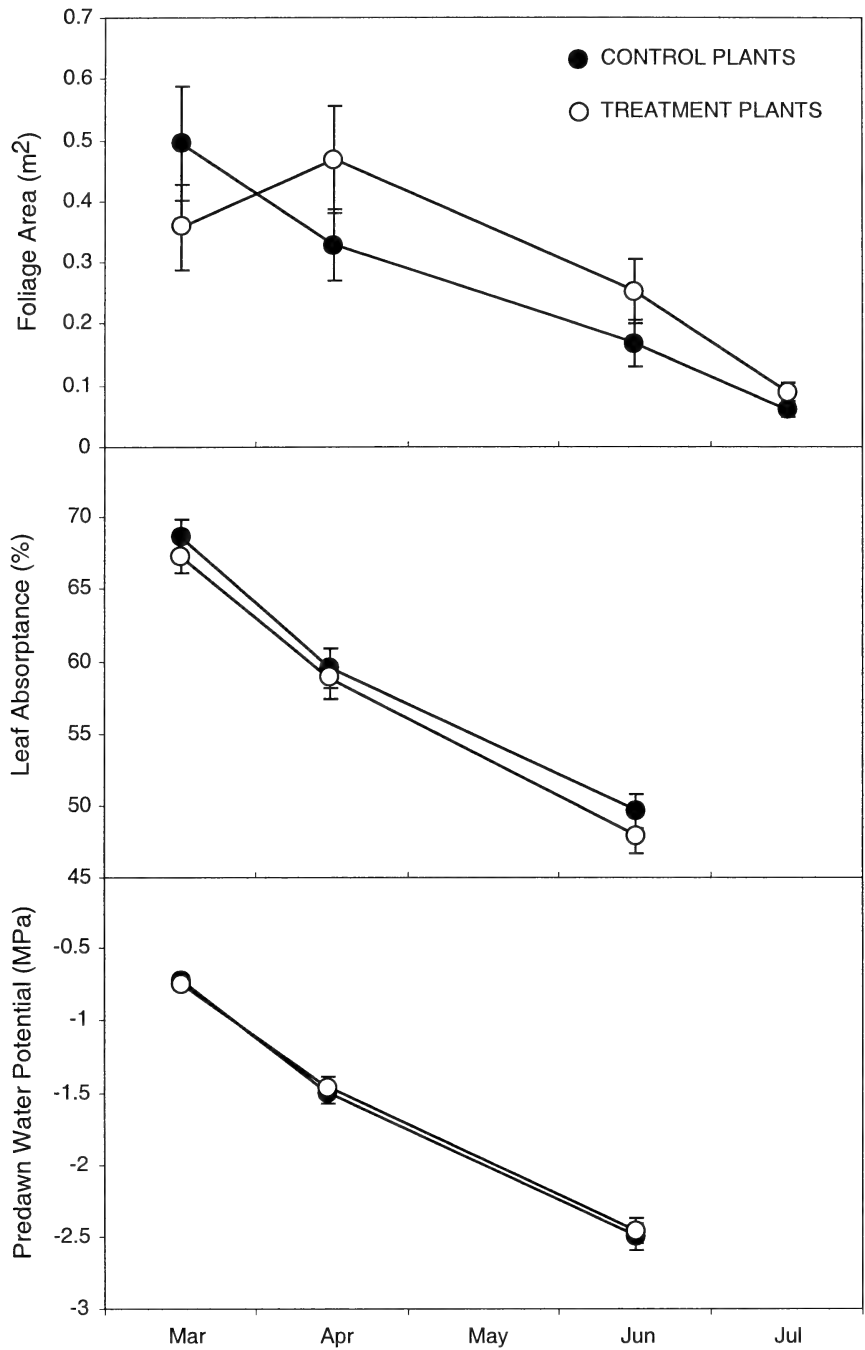


FIG. 2. Seasonal changes of mean predawn water potential, leaf absorbance and foliage area for *Encelia farinosa* control plants (closed symbols) and plants partially defoliated in March (open symbols). N = 20 plants per group. Error bars = 1 standard error.

where S is total number of stems, L_i is number of leaves for stem i, and w_{ij} is leaf width (mm) for leaf j of stem i. Three stems per plant were subjectively chosen to represent the variability of stems sizes on the plant. For each, the total number of leaves (L_i) were counted and leaf widths (w_{ij}) were measured on three leaves that represented the var-

iation of leaf sizes on the stem. The binomial coefficients in the equation (0.106 and 0.006) were empirically determined from a regression of measured leaf widths versus leaf areas on 762 leaves; the intercept was forced through zero ($R^2 = 0.985$; $P < 0.001$). This nondestructive estimate of foliage area compared well with other methods (Sandquist

TABLE 1. MEAN VALUES FOR PERCENT FOLIAGE AREA CHANGE (± 1 SE) OVER THREE TIME PERIODS FOR *ENCELIA FARINOSA* PARTIALLY DEFOLIATED (TREATMENT) AND CONTROL PLANTS. Significant differences based on ANOVAR were found for Group ($P < 0.001$), Month ($P < 0.001$), Group \times Month ($P = 0.001$) effects.

| | % Foliage area change | | |
|-----------|-----------------------|-------------|-------------|
| | March–April | April–June | June–July |
| Treatment | +25.5 (7.9) | –48.8 (4.9) | –61.2 (4.2) |
| Control | –25.0 (6.4) | –54.3 (4.0) | –54.7 (4.3) |

1995). To standardize for differences in plant size, foliage area analyses were based on percent foliage area change between months rather than on total foliage area.

Predawn (Ψ_{pd}) and midday (Ψ_{md}) water potential measurements were made 24 March, 28 April and 6 June 2001 using a Scholander-style pressure chamber (Soilmoisture Equipment Corp., Santa Barbara, CA). On the same dates, three fully expanded leaves of the most recently matured cohort were collected from each plant for determination of leaf absorptance. Leaves were stored in plastic bags with a damp towel and refrigerated until measurements could be made in the laboratory, within 5 d of collection (short-term storage has no effect on leaf absorptance value; Sandquist and Ehleringer 1997).

Leaf absorptance measurements were made within an Ulbricht-type integration sphere in which monochromatic 625 nm light was directed onto the adaxial surface of the leaf. Absorptance is the % of radiation incident on the leaf that is neither reflected nor transmitted. Measurements were made for only the 625 nm wavelength because this wavelength correlates most consistently with leaf absorptance values integrated over the entire energy spectrum (400–3,000 nm) as well as within the photosynthetically active range (400–700 nm; Ehleringer 1981).

Plant canopy volume (m^3) was calculated using the equation for a half spheroid and measurements of plant height, maximum canopy width and width

perpendicular to the maximum width. Measurements were made in March and again in June to determine relative growth over the season.

Statistics

Repeated measures analysis of variance (ANOVAR; JMP 3.1, SAS Institute Inc.) was used to evaluate differences between treatment and control groups for seasonal responses of water potential (pre-dawn and mid-day), leaf absorptance and percent change in foliage area. For all ANOVAR tests the recommendations of Potvin et al. (1990) were used for evaluation of effects due to group, month and group-by-month interaction.

A one-tailed Student's t-test was used to evaluate percent growth (March to June) differences between treatment and control groups. It was hypothesized that treatment plants would grow less than control plants owing to defoliation.

For all analyses, the assumptions of normality and equal variances were met and no transformations of data were necessary.

RESULTS

Treatment plants, after partial defoliation, started with approximately 30% less foliage area than control plants, yet after one month, the foliage area of treatment plants was 40% greater than that of control plants (Fig. 2, Table 1). As a percentage of foliage area change, control plants showed a 25% decrease between March and April whereas treatment plants increased foliage area by 25%. This compensation in leaf area resulted in a significant group effect ($P < 0.001$) and group-by-month interaction ($P = 0.001$; Table 2). The percent change over the following three months was fairly similar between groups (Table 1). By July, foliage area of both groups had converged on a very low level, although treatment plants still maintained about 30% more total foliage area than control plants (Fig. 2).

Between March and June, control plants increased in size by an average of 8.6% (± 6.1 SE), whereas treatment plants actually decreased in size

TABLE 2. SUMMARY OF ANALYSES OF VARIANCE WITH REPEATED MEASURES (F-VALUES AND SIGNIFICANCE LEVELS) FOR TRAITS COMPARED BETWEEN GROUPS (PARTIALLY DEFOLIATED VS. CONTROL) OF *ENCELIA FARINOSA* OVER FIVE MONTHS IN THE MOJAVE DESERT.

| | ANOVAR effects | | | | | |
|---------------------------|----------------|-----------|-------|-----------|----------------------|----------|
| | Group | | Month | | Group \times Month | |
| | F | P | F | P | F | P |
| Predawn Water | | | | | | |
| Potential (Ψ_{pd}) | 0.04 | 0.83 ns | 382.5 | <0.001*** | 0.18 | 0.83 ns |
| Midday Water | | | | | | |
| Potential (Ψ_{md}) | 0.86 | 0.36 ns | 244.7 | <0.001*** | 2.02 | 0.15 ns |
| Leaf Absorptance | 0.67 | 0.41 ns | 200.7 | <0.001*** | 0.27 | 0.75 ns |
| Percent Foliage Change | 15.78 | <0.001*** | 54.56 | <0.001*** | 8.27 | 0.001*** |

by more than 4.5% (± 7.0 SE). In spite of the high variances for these means, the difference between groups was significant at the $P = 0.08$ level and in the direction predicted.

Predawn water potential showed a significant decline throughout the drought period as would be expected, but there was no significant difference between the treatment and control groups (Fig. 2, Table 2). There was also no significant group \times month effect ($P = 0.83$) thereby indicating that the seasonal decline in predawn water potential was equivalent for both the control and treatment groups (Fig. 2). Similar results were also found for midday water potential (Table 2). Group and group \times month effects were not significant (Table 2), but Ψ_{md} significantly decreased ($P < 0.001$) over the course of the drought: from -1.9 MPa (± 0.05 SE) to -3.4 (± 0.05) for control plants and from -1.7 (± 0.04) to -3.4 (± 0.09) for treatment plants.

Mean leaf absorptance values in March (69% and 67% for control and treatment groups respectively) were in a range that is typically found in the early-to-middle stages of a drought (Sandquist and Ehleringer 1998), suggesting that plants had already experienced some degree of drought stress. However, the seasonal mean absorptance values were not significantly different between the treatment and control groups ($P = 0.42$). As expected, there was a significant decline in leaf absorptance from March to June (Fig. 2, Table 2), and this decline was statistically similar for both treatment and control groups (group \times month effect: $P = 0.75$).

DISCUSSION

Partial defoliation of *Encelia farinosa* plants at the outset of drought was expected to affect the water balance of the plants and thereby influence the absorptance values of leaves produced subsequent to defoliation. Because leaf absorptance couples closely with photosynthetic and energy balance aspects of the leaf (Ehleringer 1988), this predicted compensation (considered physiological compensation) might benefit a defoliated plant because it can occur rapidly and counteract the detriment of productivity loss due of defoliation (McNaughton 1983). However, drawbacks associated with physiological compensation, including greater water loss, might constrain this form of response. Indeed, no physiological compensation was found for the group of treatment plants in this study—those that were partially defoliated at the peak of foliage area production. As compared to control plants, the treatment plants had equivalent leaf absorptance values throughout the post defoliation period (Fig. 2). Compensation came, instead, through an increase in leaf production, after which foliage area of treatment plants actually exceeded that of control plants (Fig. 2). The increase in leaf production not only counterbalanced foliage loss but also resulted in water potential values that were indistinguishable

from control plants throughout the drought period (Fig. 2).

These results suggest that a plastic response of allocation to new foliage growth rather than physiological compensation is favored in *E. farinosa*. This result conflicts with findings for other desert plants, in which physiological compensation was the primary response to defoliation (Detling et al. 1979; Nowak and Caldwell 1984; Senock et al. 1991), but the results are not surprising given that there is a close relationship between energy balance, water loss and leaf morphological features for this species. Indeed, maintenance of higher leaf absorptance (through lower leaf pubescence) as part of the physiological compensation response to defoliation would threaten the temperature balance of the leaf (by absorbing too much radiation) or necessitate increased transpiration, resulting in high water loss relative to carbon gain. On the other hand, foliage compensation, with no relative change in leaf absorptance characteristics, retains the balance of efficient carbon gain vs. water loss without subjecting leaves to potentially lethal radiation absorption. Furthermore, for species in arid environments, where there is a premium on maintaining high root biomass for water uptake, it would be expected that belowground demand for photosynthate would necessitate a response that maximizes photosynthate production with the least water demand.

A number of other studies have also found that partial defoliation rarely results in changes of plant water status (e.g., Nowak and Caldwell 1984; Meinzer and Grantz 1990; Pataki et al. 1998; Hart et al. 2000). These studies suggest or demonstrate that this result stems from increased stomatal conductance and transpiration, but this may not be the case for *E. farinosa* in the current study. Although not tested directly, the absence of water potential differences in this study could plausibly result from compensatory canopy growth rather than leaf-level stomatal compensation.

Surprisingly, the consequences of increased foliage production were only marginally apparent. Treatment plants had only slightly lower total growth over the season than did control plants, and this difference was significant at only the $P = 0.08$ level. While moderate levels of defoliation may not have lasting consequences to the plant, or may even benefit it (McNaughton 1983), the probable consequences of foliage compensation, such as lower reproduction and survival or reduced productivity in subsequent years, were not measured in this study. However, there were no strong immediate costs associated with compensatory foliage growth.

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MOLECULAR DATA CONFIRM THE PHYLOGENETIC PLACEMENT OF
THE ENIGMATIC *HEPEROCALLIS* (HEPEROCALLIDACEAE)
WITH *AGAVE*

J. CHRIS PIRES¹

Jodrell Laboratory, Royal Botanic Gardens, Kew. Richmond,
Surrey TW9 3DS, U.K.

IVAN J. MAUREIRA

Department of Agronomy, University of Wisconsin, Madison, WI 53706

JON P. REBMAN

San Diego Museum of Natural History, San Diego, CA 92112

GERARDO A. SALAZAR², LIDIA I. CABRERA², MICHAEL F. FAY, AND MARK W. CHASE

Jodrell Laboratory, Royal Botanic Gardens, Kew. Richmond,
Surrey TW9 3DS, U.K.

ABSTRACT

Hesperocallis is a monotypic genus endemic to western North America, currently classified in Hesperocallidaceae (*sensu* Angiosperm Phylogeny Group 1998, 2003) but typically placed in Liliaceae (*sensu* Cronquist 1988) in floristic treatments. On the basis of DNA sequence data, the phylogenetic placement of *Hesperocallis* is demonstrated to be with Agavaceae, rather than with Alliaceae, Hemerocallidaceae, or Liliaceae as thought by earlier authors based on morphology. Based on these results, we recommend sinking Hesperocallidaceae in Agavaceae within Asparagales.

RESUMEN

Hesperocallis es un género monotípico endémico del oeste de América del Norte. Actualmente, *Hesperocallis* está clasificado dentro de Hesperocallidaceae (Angiosperm Phylogeny Group 1998, 2003); sin embargo, previas clasificaciones basadas en morfología lo han situado al interior de Liliaceae (*sensu* Cronquist 1988). Con base en secuencias de ADN, *Hesperocallis* esta filogenéticamente emparentado con la familia Agavaceae y no con Alliaceae, Hemerocallidaceae o Liliaceae como fue sugerido por previos autores. Como resultado, recomendamos considerar a Hesperocallidaceae como parte de Agavaceae dentro de las Asparagales.

Key Words: *Agave*, Agavaceae, Asparagales, *Hesperocallis*, Liliaceae, molecular systematics, phylogeny.

Asa Gray (1867) described *Hesperocallis* as a monotypic genus of Liliaceae. The sole species, *H. undulata*, occurs on sandy flats and mesas of creosote scrub in the Mojave Desert and Sonoran Desert (USA: Arizona, California, and Nevada; Mexico: central Baja California and Sonora; Wiggins 1980; McNeal 1993; Utech 2002). *Hesperocallis* is a perennial herb, with mostly basal linear leaves and a scapose inflorescence arising from a tunicate bulb. The leaves are distinctively keeled, strongly undulate, and blue-green with white margins. Commonly known as the desert glory lily, it has large white flowers that make it not only one of the most attractive desert species, but also a plant

that has attracted horticultural use (Utech 2002). Native Americans used the bulbs for food (Moerman 1986), and the early Spanish colonists called the bulbs *ajo*, due to their garlic smell. However, Gray's description of *Hesperocallis* did not note the alliaceous scent, perhaps because he described the plant from a dried specimen, collected by J.G. Cooper, a botanist with the U.S.-Mexican Boundary Survey from 1860–1861. In fact, Gray (1867) thought that *Hesperocallis* was related to *Hemerocallis*, and the generic name was intended to suggest that affinity, “along with the far western, instead of eastern habitat” (*Hesperocallis* is Greek for “western beauty”). Rowntree (1941) provided an early natural history essay of *Hesperocallis*, Maddox and Carlquist (1985) studied seed dispersal, and recent studies and floras contain descriptions and plates of *Hesperocallis* (e.g., McNeal 1993; Utech 2002). North American floras typically follow Cronquist's (1988) taxonomic scheme and continue to place *Hesperocallis* in Liliaceae; however,

¹ Current address: Department of Agronomy, University of Wisconsin, Madison, WI 53706. email: jcpires@wiscmail.wisc.edu

² Current address: Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 70-367, 04510 México, D. F., México.

recent authors have noted the artificiality of Cronquist's Liliaceae (Duvall et al. 1993; McNeal 1993; Chase et al. 1995; Reveal and Pires 2002; Utech 2002).

Hesperocallis, like many monotypic genera of petaloid monocots, has puzzled plant systematists for decades. Hutchinson (1934, 1959) placed *Hesperocallis* and *Hosta* in his Hemerocallidaceae (Liliales), separate from his order Agavales. Cave (1948, 1970) found that *Hesperocallis* was karyologically and embryologically similar to *Hosta* (Hostaceae) and some genera of Agavaceae. Even though their base chromosome numbers are different ($\bar{x} = 24$ in *Hesperocallis* and $\bar{x} = 30$ in *Hosta* and Agavaceae), they share a strongly bimodal karyotype. Although Cave (1948) suggested the removal of *Hesperocallis* and *Hosta* from Hemerocallidaceae, Hutchinson (1959) did not alter his 1934 classification of *Hesperocallis* and maintained it in Hemerocallidaceae. Dahlgren, Clifford and Yeo (1985, pg. 187) placed the North American *Hesperocallis* and *Leucocrinum* in Funkiaceae (=Hostaceae) but were uncertain about the relationship of this family to the other 29 families of their Asparagales. Later workers (Alvarez and Köhler 1987) found that the pollen grains of *Hesperocallis*, *Hosta*, and *Leucocrinum* have similar unibaculate muri that differed from the pollen morphology of genera traditionally placed in Agavaceae.

In contrast, Traub (1953, 1982) did not believe there was a close relationship between *Hesperocallis* and *Hosta* and placed *Hosta* in tribe Hosteeae of Agavaceae (Agavales *sensu* Hutchinson 1934, 1959; Traub 1953, 1972b). For *Hesperocallis*, Traub emphasized its alliaceous scent and hypothesized a relationship with Alliaceae. Traub (1968) initially placed *Hesperocallis* in its own tribe and then later in its own family Hesperocallaceae in his order Alliales (Traub 1972a, 1982). Traub (1982) referred to *Hesperocallis* and *Milula spicata* as "living fossils" and postulated that they represented ancestral lineages similar in form to the extinct ancestors of Alliales.

Hesperocallis is currently treated as the sole representative of the segregate family Hesperocallidaceae within Asparagales (Angiosperm Phylogeny Group, APG 1998; APG II 2003). APG (1998) left Hesperocallidaceae unplaced within the Asparagales because it had not been included in any molecular phylogenetic analyses. Fay et al. (2000) produced a molecular analysis of Asparagales based on *rbcL*, *atpB*, and *trnL-F* plastid DNA sequences, which clarified relationships within Asparagales and was the basis of the most recent classification of the order (APG II 2003). However, Fay et al. (2000) did not sample *Hesperocallis* and identified *Hesperocallis* as a critical taxon to be included in future studies. Fay et al. (2000) suggested that *Hesperocallis* might have affinities with Agavaceae, a reasonable hypothesis given that *Hosta* had been

found to be related to *Agave* in previous molecular studies (Bogler and Simpson 1995, 1996; Chase et al. 1995). To determine whether *Hesperocallis* has affinities with Alliaceae, Agavaceae, or Hemerocallidaceae, we present the first molecular phylogenetic analysis of *Hesperocallis* using the combined DNA matrix for Asparagales of Fay et al. (2000), to which we have added new data for *Hesperocallis*.

MATERIALS AND METHODS

Material of *Hesperocallis* was collected into silica gel using the method of Chase and Hills (1991). Two accessions of *Hesperocallis* were used in this study that were collected at different localities from within the Anza-Borrego Desert State Park, San Diego County, in southern California. One voucher is deposited at SD (Rebman 7176, SD 148685) and the other at JEPS (Cranfill & Schmid, s.n.). DNA extraction and sequencing were carried out using standard techniques (Fay et al. 2000). Newly determined *rbcL* (accession number AY561251), *atpB* (accession number AY561252), and *trnL-F* (accession number AY561253) sequences for *Hesperocallis* have been deposited in the GenBank database. Insertions/deletions (indels) were introduced to the *Hesperocallis trnL-F* sequence to align it to the matrix.

Using the parsimony algorithm of the software package PAUP* for Macintosh (version 4.0b10; Swofford 2002), a tree search was conducted on the combined *rbcL/atpB/trnL-F* matrix under the Fitch (equal weights) criterion (Fitch 1971) with 1000 random sequence additions and tree-bisection-reconnection (TBR) branch swapping, but permitting only five trees to be held at each step. All shortest trees collected in the 1000 replicates were swapped on to completion with no tree limit. Successive approximation weighting was carried out according to the rescaled retention index (RI), using the maximum value (best fit) and a base weight of 1.0. A new heuristic search was performed with 1000 random sequence additions, TBR swapping and holding five trees per step; the reweighting/heuristic search combination was repeated until the number of trees found and tree length became consistent. Internal support was evaluated with equal weights using 1000 replicates of the bootstrap (BS; Felsenstein 1985), with simple sequence addition and TBR swapping, but permitting only five trees to be held at each step.

RESULTS AND DISCUSSION

The aligned data matrices were unchanged from the original Fay et al. (2000) matrix except for the addition of the three sequences for *Hesperocallis*. The total aligned matrix was 4857 characters (*rbcL* accounted for 1428 base pairs, bp, *atpB* for 1518 bp, and the *trnL-F* region for 1911 bp, respectively). A total of 1306 base positions were excluded

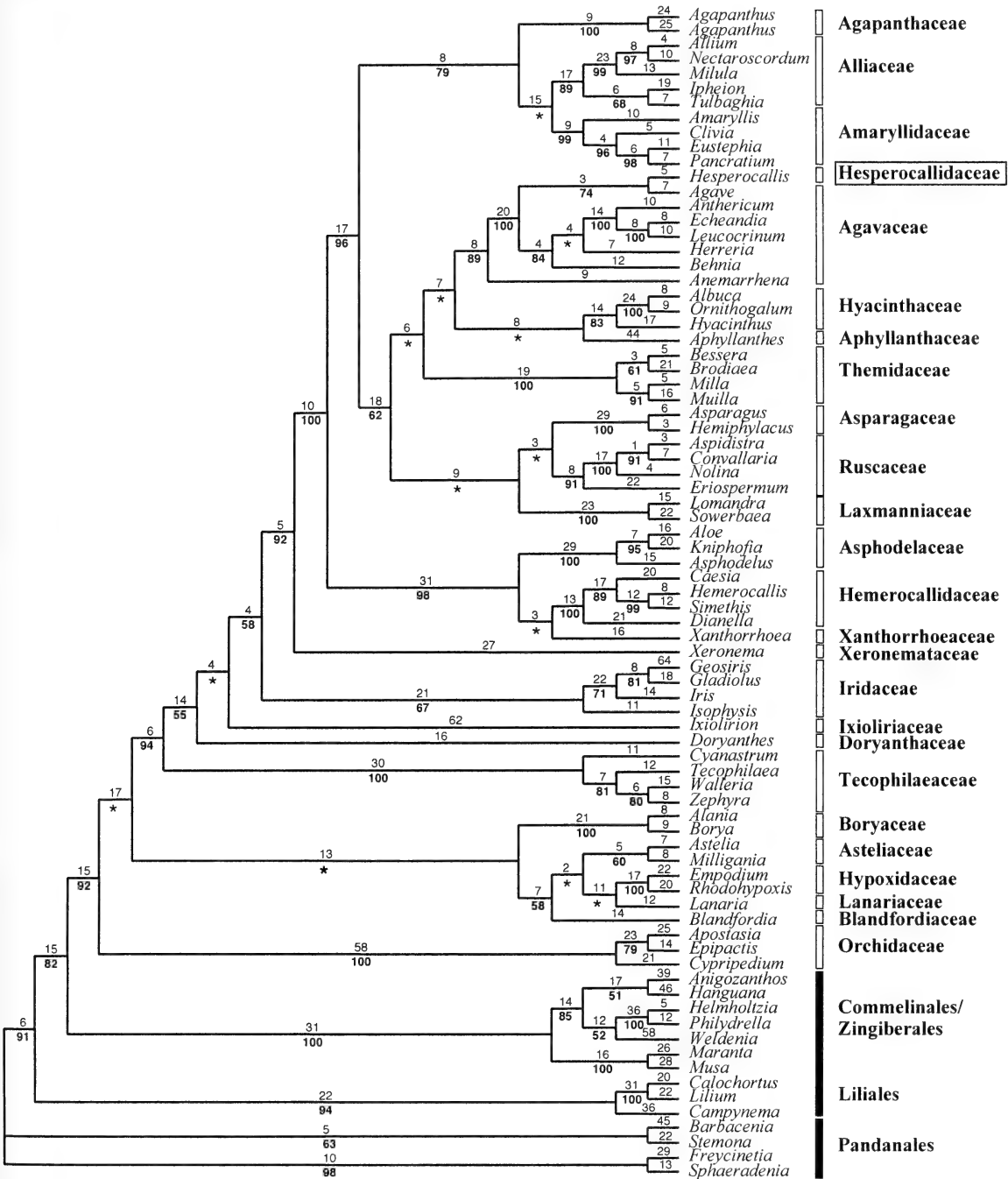


FIG. 1. Single most parsimonious tree of Asparagales (obtained after successive weighting) based on *rbcL*, *atpB*, and *trnL-F* plastid DNA sequences. Branch lengths are shown above the branches and bootstrap percentages (produced with equal weighting) are shown below the branches (asterisks indicate <50% BS). Dark bars to right of the tree indicate outgroup orders. Open bars indicate the 25 narrowly bracketed families of Asparagales (APG II 2003). Note that Hesperocallidaceae are in a clade containing Agavaceae and not with Alliaceae or Hemerocallidaceae.

either at the beginning or end of sequences or where alignment of the *trnL-F* sequences proved too difficult to align clearly (Fay et al. 2000). Of the 3551 included characters, 1479 (42%) were var-

iable and 958 (27%) were potentially parsimony in-

formative. The combined Fitch analysis produced 18 equally most-parsimonious trees, tree length (TL) =

4721, consistency index (CI) = 0.43 and retention index (RI) = 0.55. One of these trees was selected as optimal under the weighting criterion, 2229 weighted steps, CI = 0.55 and RI = 0.69 (Fig. 1, with its Fitch branch lengths shown above the branches and bootstrap percentages, BS, below). As expected, the overall topology of the tree is similar to that found by Fay et al. (2000). *Hesperocallis* was moderately supported as sister to *Agave* (74% BS), but strongly supported (100% BS) as being a member of a clade that included Agavaceae (*sensu* APG 1998), Anthericaceae, Behniaceae, and Herreriacae. Together, these taxa formed a sister group to Anemarrhenaceae (89% BS). Indels (not coded in the matrix) also supported the relationship of *Hesperocallis* with *Agave*.

The data presented here provide clear evidence that *Hesperocallis* is related to Agavaceae rather than members of Alliaceae or Hemerocallidaceae. In terms of APG (1998), *Hesperocallis* is embedded in a clade that includes Agavaceae, Anemarrhenaceae (monogeneric), Anthericaceae, and Behniaceae (monogeneric). In contrast to APG (1998), the APG II (2003) classification expands Agavaceae to include Anemarrhenaceae, Anthericaceae, Behniaceae and Herreriacae. Based on our results (Fig. 1), we recommend that Hesperocallidaceae be treated as a synonym of Agavaceae (*sensu* APG II 2003) in the higher Asparagales.

However, making Hesperocallidaceae synonymous with Agavaceae is complicated by the fact that APG II has a "bracketed system" for the classification of the higher Asparagales. This system allows for the option of smaller bracketed families (such as the expanded Agavaceae) to be recognized within larger families of the APG II system. Specifically, APG II (2003) further simplified the higher Asparagales into two newly circumscribed large families, Asparagaceae s.l. and Alliaceae s.l. In this sense, Agavaceae (with *Hesperocallis*) would simply be within Asparagaceae s.l., along with Aphyllanthaceae, Asparagaceae, Hyacinthaceae, Laxmanniaceae, Ruscaceae and Themidaceae.

Future studies will resolve the phylogenetic relationship of *Hesperocallis* to other taxa such as *Camassia*, *Chlorogalum*, *Hosta*, *Hesperaloe*, *Hesperoyucca*, and the other genera of the *Agave-Yucca* clade (Bogler and Pires unpublished data).

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GROWTH RESPONSE OF *CORTADERIA SELLOANA* AND *CORTADERIA JUBATA* (POACEAE) SEEDLINGS TO TEMPERATURE, LIGHT, AND WATER

ALISON E. STANTON

BMP Ecosciences, 2114 33rd Ave, San Francisco, CA 94116

JOSEPH M. DiTOMASO¹

Weed Science Program, Department of Vegetable Crops, Robbins Hall,
University of California, Davis, CA 95616

ABSTRACT

Cortaderia selloana (pampasgrass) and *Cortaderia jubata* (jubatagrass) are South American perennial grasses species that have escaped cultivation in California and become aggressive invasive species, particularly in coastal environments. Both are characterized by large mounded tussocks, long serrated leaves, and feathery, plume-like inflorescences. While *C. jubata* is currently restricted to coastal areas in central and northern California, invasive populations of *C. selloana* can be found both along the warmer coastline of southern California and within interior regions of the state. To better understand the potential geographic distribution of these species in California we examined seedling growth responses to varying environmental factors, including light, temperature, and moisture conditions typical to both coastal and inland California sites. Under growth chamber conditions, both species grew optimally at 20°C. However, *C. selloana* seedlings had significantly greater height and leaf area compared to *C. jubata* at both 20 and 25°C. While temperature did not significantly affect *C. selloana* survivorship, mortality of *C. jubata* seedlings was ≥90% at temperatures above 25°C. Using shade cloth to control light intensity, *C. selloana* seedlings grew more vigorously than *C. jubata* under the higher light regimes, producing 234% more biomass at full sun. While the relative growth rate of *C. selloana* increased linearly with increasing light intensities, reaching a maximum of 21.4 mg g⁻¹day⁻¹ at 1600 μmol m⁻²s⁻¹, *C. jubata* growth rate reached a maximum of 12.7 mg g⁻¹day⁻¹ at 60% full sunlight (960 μmol m⁻²s⁻¹) and did not increase at higher light intensity. Drought significantly reduced growth of both species, but *C. selloana* was more tolerant of moderate drought than *C. jubata*. The mean dry weight of *C. selloana* seedlings was twice that of *C. jubata* when water was withheld for 27 days. When containers were maintained at varying ranges of soil moisture, *C. selloana* seedlings grew significantly taller and had higher leaf area and average dry weights than *C. jubata* at moderate drought conditions. The response to temperature, light, and moisture suggests *C. selloana* has greater potential invasiveness than *C. jubata* in both coastal and inland areas within the state, particularly in warmer regions. *Cortaderia selloana* growth was more vigorous than *C. jubata* under optimal conditions and also demonstrated greater drought tolerance and higher survivorship at increased temperatures and light intensity.

Key Words: California, *Cortaderia*, invasive, light, temperature, wildland.

Two South American species of *Cortaderia* have naturalized and become invasive in California. *Cortaderia selloana* (J.A. & J.J. Schult.) Asch. & Graebn. (pampasgrass) is native to Argentina, southern Brazil, and Uruguay, and *Cortaderia jubata* (Lemoine) Stapf. (jubatagrass, occasionally called pampasgrass or pin pampasgrass) is native to the Andes of Bolivia, Ecuador, and Peru (Connor and Edgar 1974). Both species cover extensive areas in their native range on plains, open slopes, and along river margins. They are large perennial grasses that form mounded tussocks of sharply serrated leaves with feathery, plume-like inflorescences that extend above the foliage on tall culms. The massive underground root structures are long-lived, reportedly surviving at least 40 years (Costas-Lippmann 1976).

In part because of their showy plumes, both spe-

cies were introduced to California through the nursery trade in Santa Barbara in the mid 1800s (Costas-Lippmann 1977). *Cortaderia selloana* was planted more extensively than *C. jubata*, but both species have escaped cultivation and spread throughout the state. In addition to its ornamental uses, *C. selloana* (and possibly *C. jubata*) was planted by the Soil Conservation Service in Ventura County in the 1940s for erosion control and as supplemental dry land forage (Costas-Lippmann 1977). It has also been used for similar purposes in Australia, New Zealand, and Tasmania (Gadcil et al. 1984; Rawling 1988; Harradine 1991).

The primary physiological difference between the two species is their reproductive strategy. Populations of *C. jubata* consist of entirely female plants that produce seed apomictically (Conner 1972). In apomixis, seeds develop asexually without any pollination, resulting in seeds that are genetically identical to the parent plant. In contrast, *C. selloana* is functionally dioecious, producing

¹ Author for correspondence, e-mail: ditomaso@vegmail.ucdavis.edu.

seed through typical pollination of the female flowers (Conner 1972). Seed production is prolific in both species; Drewitz (2000) estimated that a single *C. jubata* inflorescence could produce up to 120,000 seeds. Airborne seeds are reported to disperse 20 miles in the wind (Harradine 1991).

Although it was widely recognized in the literature that *C. jubata* was an aggressive invasive weed, only recently has *C. selloana* been regarded as a widespread invasive species of wildlands (DiTomaso et al. 1999). Both species thrive on the California coast where fog is common, summertime temperatures are moderate, and winters are wet with little or no frost. Currently, *C. jubata* has a strictly coastal distribution in central and northern California. Invasive populations of *C. selloana* are concentrated along the warmer coastline south of Santa Barbara County (DiTomaso et al. 1999), but have been shown to have greater invasive potential than *C. jubata* (Lambrinos 2001). In addition to invading coastal habitats, *C. selloana* has also expanded its range into interior regions and has occupied a greater diversity of habitat types in California than *C. jubata*. In these warmer and drier interior climates, *C. selloana* can be found in wetlands, riparian corridors, and other waterways (Lambrinos 2001). Thus, we hypothesize that *C. selloana* is better adapted to higher light and temperatures compared to *C. jubata*.

Lambrinos (2000) attributed the invasiveness of *C. selloana* to its system of out-breeding and a greater ability to adapt to different selective regimes. Costas-Lippmann and Baker (1980) found significant allozyme variation across five different enzyme systems for *C. selloana* populations in California, but *C. jubata* did not exhibit any allozyme variation among populations. The greater genetic diversity of *C. selloana* may allow for more ecotypic flexibility and may contribute to its continued invasive success and ability to infest a wide variety of climates and habitats. In contrast, the apomictic strategy of *C. jubata* is likely advantageous in founding populations when colonizing new areas, because a single individual can produce copious seed. However, *C. jubata* has little opportunity for adaptation to new environments through genetic recombination. Consequently, the capacity for *C. jubata* to expand its range beyond its current coastal distribution may be limited, while *C. selloana* may be poised to expand within both inland and coastal regions.

Large populations of both species can displace native plants, impact wildlife habitat, reduce access to recreational areas and can become a significant fire hazard (Lambrinos 2000). They have also been shown to reduce conifer establishment and growth in logging operations (Fuller 1976; Gadgil et al. 1990). Because of their ecological impacts in natural areas, the California Exotic Pest Plant Council (currently California Invasive Plant Council) has listed both species among the most widespread in-

vasive wildland plants in California (Howald et al. 1999). In addition to California, both *C. jubata* and *C. selloana* are also considered invasive in Australia, New Zealand, and South Africa (Rawling 1988; Harradine 1991).

The objectives of this study were to compare the growth responses of *C. jubata* and *C. selloana* seedlings to varying conditions of light, temperature, and moisture typical to both coastal and inland California conditions. From these results, we hope to better understand the environmental conditions that influence seedling establishment and potential geographic distribution of both species in California. These findings may have important implications for predicting where seedlings are likely to establish and where detection and prevention programs should be focused.

MATERIALS AND METHODS

Plant Material

For all *C. jubata* experiments, seeds were collected in California at Vandenberg Air Force Base (VAFB), Santa Barbara County and at Big Lagoon, Humboldt County. The seeds from VAFB were designated as a southern population and seeds from Big Lagoon a northern population. The experimental results from the two populations were not statistically different and only combined results are presented. *Cortaderia selloana* seeds used in the temperature experiments were collected at Vandenberg Village, near VAFB, and seeds used for the light intensity, drought, and moisture stress experiments were purchased from the Mistletoe Seed Company in Santa Barbara County.

For each experimental year, fresh plumes on mature plants were collected in the field the previous fall. Only seeds less than one year old were used for all experiments. Seeds were removed from the inflorescences, stored in paper bags in the laboratory at room temperature and used as needed.

Growth Conditions and Harvest Procedures

Temperature. Seeds were sown on the surface of Yolo Fine Sandy Loam (YFSL) in black plastic trays (51 holes per tray) on March 11, 2000. Plants were grown in the greenhouse under natural light and subirrigated daily with 5% Hoagland's solution. After one week, seedlings were thinned to one per hole and grown for an additional two weeks. Daily day/night greenhouse temperatures averaged 24 and 18°C, respectively, during this period. Twenty-one days after planting, three flats (one northern and southern *C. jubata* population, and one *C. selloana*) containing a variable number of plants were transferred to each of six controlled temperature rooms. Plants were grown in a growth chamber at constant temperatures of 10, 15, 20, 25, 32 or 37°C for two months under fluorescent bulbs set to a 12 hr photoperiod. Light levels averaged 75 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$

photosynthetic photon flux density (PPFD) with no significant differences across all six chambers. Soil was kept moist with a weak nutrient solution.

A pretreatment baseline harvest was conducted using 6 to 8 replicates per flat, with individual plants serving as replicates. Measurements included plant height, number of leaves, and number of stem tillers, as well as the number of surviving seedlings. Plants were clipped at the soil surface and evaluated for leaf area with a LICOR Model LI-3100 Leaf Area Meter. Aboveground biomass was dried at 32°C for 2 wk and then weighed. Measurements were taken on the remaining plants every two weeks and all plants were harvested after 8 wk and evaluated as described above. Data are reported only for the 8-wk harvest timing.

Light intensity. For all greenhouse experiments, seeds were planted on the soil surface in one gallon black plastic pots filled with YFSL. Seedlings were thinned to one per pot and grown in a greenhouse of the Vegetable Crops Department at the University of California, Davis. Pots were irrigated as needed with tap water.

Light intensity in the greenhouse averaged 1600 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD. Daily day/night greenhouse temperatures averaged 29 and 22°C, respectively. Shade treatments were applied on June 29, 1999, 21 d after planting. Black nylon mesh shade cloths were fitted to PVC frames to reduce light intensity to 60, 30, and 15% of available light (average of 960, 450, and 230 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD, respectively). The frames enclosed plants on all sides at a height of 1.5 meters. Twenty pots of each species were randomly placed under each frame so there was one treatment per bench, with 40 pots (divided into two rows) for a total of 160 pots. An additional 10 pots of each species were planted for a pretreatment baseline harvest. Shade treatments were randomly assigned to a bench and no significant light or temperature gradients were measured among the benches.

For baseline values, 10 replicates of each species were harvested from each of the four treatments at 21 d after planting (before initiation of treatment). Plant height, number of leaves, and number of stem tillers were measured and then plants were clipped at the soil surface, dried and weighed. For the pretreatment baseline harvest, the plants were very small so whole plants were used for leaf area determination. After measurements were taken in the subsequent 4- and 8-wk harvests times, but only the 8-wk harvest data are presented. Entire plants were removed from the soil and the roots were excised from the shoots. The leaf blades were then separated from the sheaths and culms at the collar. Roots were washed free of soil, and above and below ground plant parts were dried at 32°C for 48 hr before weighing. Leaf blades separated from the shoots at the collar were analyzed for leaf area as

described above, then dried and weighed. Only data from 8-wk harvest are presented.

Moisture stress. Moisture experiments were initiated 39 d after planting. All pots were watered to excess with tap water and allowed to drain overnight. Species were randomly assigned one of four drought treatments with 12 replicated pots per treatment. One treatment included a fully watered control. Control plants were measured at each new drought period to serve as an indicator of unstressed growth. Plants exposed to intermediate drought stress were not watered for 6 d, watered each day for 8 d, then again not watered for an additional 27 d. Plants exposed to a sustained drought period did not receive any additional water for 41 d. In the fourth treatment, plants were not watered for 12 d, watered once, and then allowed to dry until they became necrotic. These plants were used to obtain lethal water content (LWC). Plant height, number of leaves, and the number of stem tillers were measured in all plants.

It was not possible to determine the effects of the different drought periods directly on soil water potential because normal soils tensiometers are only useful in the range from 0.0 to -0.08 MPa (Kramer and Boyer 1995) and moisture levels in this experiment fell well below this range. Consequently, the relative water content (RWC) was determined in a subset of the replicates.

After the final growth measurements in all twelve replicates, six plants of both species were used to determine the effect of different drought periods directly on plant water status in each treatment. The remaining six replicates in each treatment were returned to container water capacity and monitored for survival and recovery for one week.

For the RWC analysis, the above ground plant was cut at soil level and immediately weighed. After weighing, the entire plant was placed under water and a fresh cut was made on the basal stems, and the entire plant was placed in a plastic bag filled with distilled water and allowed to saturate in a cool, dark chamber. After 24 hr, each plant was removed from the water, patted dry, and reweighed. The plants were then placed in an oven for 24 hr at 32°C before obtaining the final dry weight. RWC was determined according to the formula from Kramer and Boyer (1995):

$$\text{RWC} = \frac{\text{Fresh weight at harvest} - \text{Dry weight}}{\text{Saturated weight} - \text{Dry weight}}$$

Lethal water content (LWC) was determined for plants that had become necrotic according to the formula:

$$\text{LWC} = \frac{\text{Fresh weight at harvest} - \text{Dry weight}}{\text{Dry weight}}$$

In a second moisture stress experiment, pots containing twelve-wk-old seedlings were fully watered and allowed to drain for 24 hr. The soil surface was

sprinkled with 50 g of sand to prevent crusting and cracking during the drought treatment and the pot, plant, and soil were weighed to obtain an initial pot weight at container capacity. Container capacity (23% water \pm 4%) was previously determined as the average amount of water remaining in the pot (10 replicates) after gravity drainage according to the method of Singer and Munns (1996). We recognize that container capacity in pot experiments may not be the same as field capacity because capillary columns are often shorter in pots than in field conditions (Kramer and Boyer 1995). However, the relative differences among treatments should provide an approximation of field conditions.

In this experiment, full light intensity in the greenhouse averaged 900 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ PPFD. Daily day/night greenhouse temperatures averaged 22 and 17°C, respectively. Because of the timing of this experiment (November 1, 2000), light levels were significantly lower than the light intensity experiment conducted during the summer (June 29, 1999).

Prior to initiating treatments, six replicates per species were evaluated as previously described and harvested to obtain pretreatment baseline values for plant height, dry weight, and number of leaves. Seven replicates per species were randomly assigned to one of four moisture treatments: 1) 100–75%, 2) 75–50%, 3) 50–25%, and 4) less than 25% of container capacity, as determined by fractions of the initial pot weight. During the experiment, pots were allowed to dry to the low end of their container capacity range. This corresponded to 0, 5, 10, and 37 d without water for treatments 1, 2, 3 and 4, respectively. After the initial drying periods, plants were returned to the upper end of their container capacity range on a regular basis (usually every three days) by adding water to the pot until the initial pot weight was achieved. Plants were maintained under these moisture regimes for 8 wk before being harvested as previously described. Plant height, leaf number, leaf area and above ground biomass were evaluated.

Growth Analysis and Statistical Procedures

For seedling mortality values at various temperature conditions the individual replicates were analyzed between both species for each temperature using a chi-squared test (χ^2 value).

Mathematical growth analyzes were used to evaluate the effects of light and temperature on dry matter production and biomass partitioning into leaves, stems, and roots. Mean relative growth rate (RGR) was calculated for unpaired plants as the change in total dry weight over time (Evans 1972). For net assimilation rate (NAR), calculations were based on the formula from Causton and Venus (1981), which avoids the need to pair plants between harvests. NAR is calculated as the change in weight over time as a function of the assimilatory

area. Leaf area ratio (LAR) was also calculated based on the formula from Evans (1972) as the relationship between leaf area and shoot dry weight. In the light experiment, a simple regression analysis was used for all data points and light was treated as a quantitative variable in order to evaluate the effects of light on biomass partitioning and relative growth rates. Graphs with regression curves include only means to simplify presentation.

Data for the two species were subjected to separate analyses of variance (ANOVA) to determine significant treatment effects. Scheffe's multiple comparison test was used to determine significant differences among the mean values for each species ($P < 0.05$). For each treatment, pairwise comparisons were made with Scheffe's test to determine if means differed significantly between the species ($P < 0.05$). The species effect was not tested between different treatments. All analyses were carried out using Statview® 5.1 software from SAS Institute Inc.

RESULTS

Temperature

Under growth chamber conditions, both *C. selloana* and *C. jubata* had significantly higher biomass at 20°C (Fig. 1). Growth was greatly reduced at both high and low temperature extremes. After 8 wk of temperature treatment, *C. selloana* seedlings had significantly greater height and leaf area compared to *C. jubata* at both 20 and 25°C (Table 1). At 20°C, *C. selloana* also had greater numbers of leaves and tillering stems than *C. jubata* (Table 1). There were no significant differences in the measured variables of the two species at all other temperatures.

The RGR of both species peaked at 20°C (Table 1). *Cortaderia selloana* grew significantly faster than *C. jubata* under optimal temperatures. The mean RGR of *C. selloana* was 74 and 67% greater than *C. jubata* at 20 and 25°C, respectively. Seedlings of *C. jubata* had a significantly greater leaf number (12.0), stem tiller number (1.9), leaf area (24.5 cm²), RGR (1.7 mg g⁻¹ day⁻¹), and dry weight (128 mg) growing at 15°C compared to seedlings growing at 25°C (8.0, 1.0, 12.9 cm², 0.9 mg g⁻¹ day⁻¹ and 53 mg, respectively), indicating an optimal temperature range of 15–20°C (Table 1 and Fig. 1). In contrast, the height, leaf number, leaf area, RGR, and dry weight of *C. selloana* seedlings at both 15 and 25°C were significantly lower compared to those at 20°C. Furthermore, the average height of *C. selloana* seedlings was nearly twice as high when grown at 25°C compared to 15°C. This suggests that optimal growth of *C. selloana* occurs at around 20°C.

While temperature did not significantly affect *C. selloana* survivorship, *C. jubata* mortality increased significantly at temperatures above 25°C. At these higher temperatures, survival of *C. jubata* seedlings

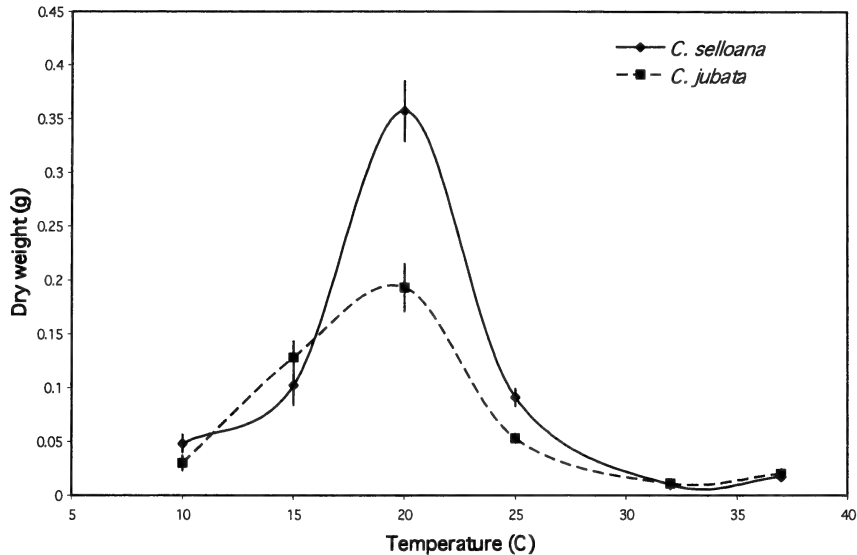


FIG. 1. Temperature effect on average dry weight of *C. selloana* and *C. jubata* under growth chamber conditions. Data are means \pm SE.

was 10% or less, whereas *C. selloana* seedling survival was 63 and 52% at 32 and 37°C, respectively (Fig. 2).

Light

Vegetative growth and biomass partitioning. A regression analysis showed a linear increase in *C. selloana* RGR (roots and shoots) after 8 wk of growth as light intensity increased up to the maximum light level of 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 3). Average total dry weight of *C. selloana* seedlings reached 2.36 g under 1600 $\mu\text{mol m}^{-2} \text{s}^{-1}$, 65% higher than plants growing at 960 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (1.5 g) (Table 2). In contrast, *C. jubata* achieved optimal growth at 960 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (60% available light). Average *C. jubata* total dry weight was 1.02 g and did not increase with the additional light in the full sun treatment (Table 2). In addition, *C. jubata* plant height was significantly reduced under

high light intensity (33.1 cm) compared to seedlings exposed to lower light levels (average of 53.5 cm at three lower light levels) (Table 3). By comparison, light level did not significantly affect plant height in *C. selloana* (average height 67 cm).

Cortaderia selloana was more vigorous than *C. jubata* under high light conditions, producing nearly two and a half times as much biomass at full sun (Table 2). Leaf area, LAR, and NAR were also significantly greater in *C. selloana* at full sun compared to *C. jubata* (Table 3), but the number of tillering shoots and leaves was not significantly different at any light level (personal observation). Regardless of the light intensity, *C. selloana* seedlings were always significantly taller than *C. jubata*.

Growth analysis. For the growth interval from 0–8 wk, the RGR of *C. jubata* increased with increasing light intensity up to a maximum rate of 12.7 $\text{mg g}^{-1} \text{day}^{-1}$ at 960 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Fig. 3).

TABLE 1. EFFECTS OF TEMPERATURE (°C) ON GROWTH AND RELATIVE GROWTH RATES (RGR) OF *C. JUBATA* AND *C. SELLOANA* GROWN FOR 8 WEEKS UNDER GROWTH CHAMBER CONDITIONS. Pooled results from northern and southern California populations are shown for *C. jubata*. Results are presented only for 15, 20 and 25°C. No statistical differences were measured among growth parameters of the two species at all other temperatures. Each data point represents the mean of at least 12 replicates. * Within each column, different letters indicate a significant difference ($P \leq 0.05$) among temperature treatments within a species according to Scheffe's multiple comparison test. Bolded and italicized values indicate significant difference ($P < 0.05$) between the two species.

| Species | Temperature (°C) | Height (cm) | Leaf no. | Tiller no. | Leaf area (cm ²) | RGR (mg g ⁻¹ .day ⁻¹) |
|--------------------|------------------|---------------|----------------|--------------|------------------------------|--|
| <i>C. jubata</i> | 15 | 25.3 b* | 12.0 a | 1.9 a | 24.5 a | 1.7 b |
| | 20 | 41.7 a | 10.1 ab | 1.3 b | 32.3 a | 3.1 a |
| | 25 | 24.8 b | 8.0 b | 1.0 b | 12.9 b | 0.9 c |
| <i>C. selloana</i> | 15 | 25.5 c | 11.2 b | 2.1 a | 21.1 b | 1.9 b |
| | 20 | 63.0 a | 16.2 a | 2.8 a | 53.1 a | 5.4 a |
| | 25 | 44.3 b | 8.2 b | 1.1 b | 23.2 b | 1.5 b |

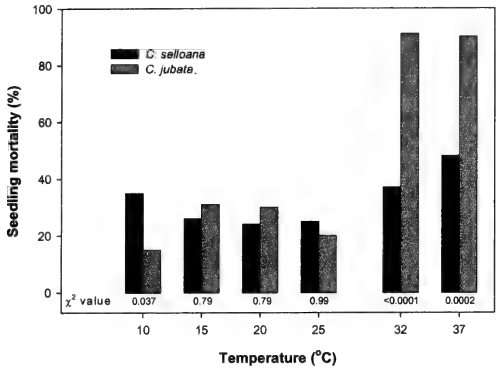


FIG. 2. Percent mortality of *C. selloana* and *C. jubata* seedlings after 8 weeks in the growth chamber. Each species was initially represented by 25 to 50 seedlings at each temperature. Chi squared values for significance are indicated below the bars.

The RGR did not increase further at full available sunlight ($1600\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$). A similar pattern was seen in net assimilation rate (NAR) (Table 3). The leaf area ratio (LAR) remained constant between 60 and 100% light intensity, indicating that plants reached photosynthetic light saturation (Table 3).

In contrast, the RGR of *C. selloana* increased linearly with increasing light intensities (Fig. 3). Seedlings with full available sun reached a maximum growth rate of $21.4\text{ mg g}^{-1}\text{ day}^{-1}$ (70% greater than *C. jubata*) over the growth interval from 0–8 wk. When light intensity increased from $960\text{ }\mu\text{mol m}^{-2}\text{ s}^{-1}$ a decline in LAR was apparently offset by a 36% increase in NAR, which reached a peak value of $3.04\text{ mg cm}^{-2}\text{ day}^{-1}$ at full sun (Table 3). Thus, the RGR continued to increase as light intensity increased and *C. selloana* did not reach a light saturation point. This indicates that

C. selloana seedlings adjusted to high light conditions through increased photosynthetic efficiency. Consequently, *C. selloana* seedlings in full sun were more physiologically active than *C. jubata* and attained a much greater size.

Drought

Moisture is often a critical factor in plant establishment in the Mediterranean climatic regions of California. Protracted summer drought makes it difficult for young seedlings to survive to maturity. Both species demonstrated high drought tolerance in the greenhouse experiments, with some seedling plants of each surviving up to 41 d without water. The drought treatments significantly reduced the RWC of 12 wk old seedlings. Fully watered controls of both species had an average RWC greater than 88%. Moderate drought reduced the RWC to 47.4% and 41.8%, and sustained drought to 28.4% and 31.8%, for *C. jubata* and *C. selloana*, respectively.

Drought significantly reduced growth of both species, but *C. selloana* was more tolerant of moderate drought than *C. jubata* (Fig. 4). The mean dry weight of 12 wk old *C. selloana* seedlings was twice that of *C. jubata* (0.75 g compared to 0.37 g) when water was withheld for 27 d. Average dry weight of moderately stressed plants was 55% lower than control plants in *C. jubata*, compared to a 33% reduction in *C. selloana*. This difference corresponded to the pattern of leaf production. Under moderate drought, *C. jubata* leaf production declined 50%, from 18 leaves per plant in the full water treatment to only 9 leaves per plant in the 27 d drought period (Fig. 5). In contrast, moderate drought did not significantly affect *C. selloana* leaf production, both fully watered and moderately stressed plants had between 12–13 leaves. Drought

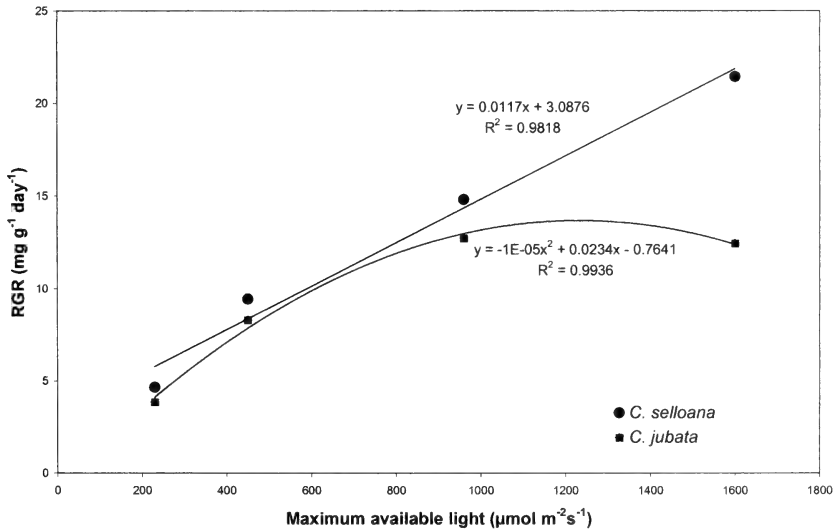


FIG. 3. Light effects on relative growth rates (RGR) of *C. selloana* and *C. jubata* after 8 wk of treatment.

TABLE 2. EFFECTS OF LIGHT ON *CORTADERIA* ROOT, LEAF AND SHOOT, AND TOTAL DRY WEIGHT AFTER 8 WEEKS IN THE GREENHOUSE. Each data point represents the mean of 10 replicates. * Within each column, different letters indicate a significant difference ($P \leq 0.05$) among light treatments within a species according to Scheffe's multiple comparison test. Bolded and italicized values indicate significant difference ($P < 0.05$) between the two species.

| Species | Light ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) | Root dry wt (g) | Shoot and leaf dry wt (g) | Total dry wt (g) |
|--------------------|--|--------------------|------------------------------|---------------------|
| <i>C. jubata</i> | 230 | 0.06 b* | 0.19 c | 0.25 c |
| | 450 | 0.25 b | 0.36 b | 0.61 b |
| | 960 | 0.59 a | 0.43 a | 1.02 a |
| | 1600 | 0.56 a | 0.45 a | 1.01 a |
| <i>C. selloana</i> | 230 | 0.06 c | 0.26 c | 0.31 d |
| | 450 | 0.26 c | 0.48 b | 0.74 c |
| | 960 | 0.72 b | 0.71 a | 1.43 b |
| | 1600 | 1.42 a | 0.94 a | 2.36 a |

also reduced average plant height in both species but *C. selloana* was significantly taller than *C. jubata* even in the control plants not exposed to drought (Fig. 6).

Stem tiller number, LWC (amount of water remaining in plants at necrosis), and mortality were not significantly different between the two species. The LWC of *C. jubata* and *C. selloana* was 0.13 ± 0.05 and 0.16 ± 0.08 g, respectively. Based on the similar LWC values, mortality rates were expected to be similar. Mortality of *C. selloana* and *C. jubata* after 41 d of sustained drought was 33 and 42%, respectively.

Soil Moisture Content

After 8 wk, soil moisture regimes greater than 25% container moisture capacity did not significantly affect RGR of either species. Relative growth rates of 20 wk old seedlings averaged $11.7 \text{ mg g}^{-1} \text{ day}^{-1}$ and $13.9 \text{ mg g}^{-1} \text{ day}^{-1}$ in *C. jubata* and *C. selloana*, respectively, when soil moisture content was greater than 25% (Table 4). Despite similar growth rates, *C. selloana* seedlings grew significantly taller and had significantly higher leaf area and average dry weights than *C. jubata* at the two moderately moisture conditions (50 and 75%). At these soil moisture ranges, *C. selloana* plants

were on average 77 cm tall, with 100.5 cm^2 leaf area, and 1.66 g dry weight while *C. jubata* plants averaged 62.5 cm tall, 82 cm^2 leaf area, and only 1.34 g dry weight (Table 4). Leaf and tiller counts were not significantly different in any treatment.

Only severe soil moisture depletion at <25% soil moisture lowered relative growth rates and reduced plant height and dry weight in both species. The average dry weight of *C. selloana* and *C. jubata* seedlings at 25% soil moisture was 67 and 64% lower, respectively, than the combined average for soil moistures above 25%. This suggests that beyond this minimum threshold, water availability is not limiting plant growth.

DISCUSSION

This study suggests that a combination of physiological and morphological factors make *C. selloana* potentially more invasive than *C. jubata*. Based on these results, *C. selloana* growth is more vigorous than *C. jubata* under optimal conditions. *Cortaderia selloana* demonstrated greater survivorship at high temperatures, an ability to utilize higher light intensities, and greater drought tolerance than *C. jubata*.

Temperature is one of the most important environmental factors limiting the geographic distribu-

TABLE 3. EFFECTS OF LIGHT ON *CORTADERIA* HEIGHT, LEAF AREA, LEAF AREA RATIO (LAR = LEAF AREA/TOTAL PLANT DRY WT), AND NET ASSIMILATION RATE (NAR = PLANT GROWTH RATE/DAY) AFTER 8 WEEKS IN THE GREENHOUSE. Each data point represents the mean of 10 replicates. * Within each column, different letters indicate a significant difference ($P \leq 0.05$) among light treatments within a species according to Scheffe's multiple comparison test. Bolded and italicized values indicate significant difference ($P < 0.05$) between the two species.

| Species | Light ($\mu\text{mol m}^{-2} \text{ s}^{-1}$) | Height (cm) | Leaf area (cm^2) | LAR ($\text{cm}^2 \text{ g}^{-1}$) | NAR ($\text{mg cm}^{-2} \text{ day}^{-1}$) |
|--------------------|--|----------------|--------------------------------|---|---|
| <i>C. jubata</i> | 230 | 56.1 a* | 36.6 a | 144.4 a | 0.61 c |
| | 450 | 56.8 a | 51.4 a | 86.8 b | 1.01 b |
| | 960 | 47.5 a | 48.5 a | 48.5 c | 1.85 a |
| | 1600 | 33.1 b | 46.3 a | 46.3 c | 1.91 a |
| <i>C. selloana</i> | 230 | 67.8 a | 41.8 b | 134.9 a | 0.54 d |
| | 450 | 73.4 a | 53.1 ab | 73.1 b | 1.16 c |
| | 960 | 70.3 a | 60.7 ab | 46.9 c | 1.96 b |
| | 1600 | 60.1 a | 69.7 a | 28.7 d | 3.04 a |

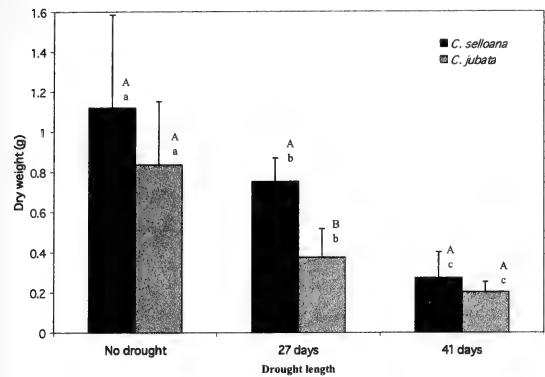


FIG. 4. Effect of drought on average dry weight of *C. selloana* and *C. jubata* under greenhouse conditions. Bars represent standard deviation. Upper case letters differing within each treatment represent significant difference ($P < 0.05$) between the two species. Lower case letter differing among treatments represent significant differences within a species.

tions of plants, determining the time of year during which growth and reproduction may occur, and regulating rates of plant growth and development (Patterson 1985). The greater temperature tolerance of *C. selloana* probably contributes to its success as an ornamental, as well as its invasive potential, in inland areas. In addition, it may provide an explanation for its concentrated distribution in southern California. Although young seedlings growing actively in the spring are unlikely to experience these high temperatures under natural conditions, the apparent inability to withstand high temperatures may partially explain why *C. jubata*, but not *C. selloana*, is restricted to coastal areas (particularly central and northern) and has failed to establish in inland sites. Young *C. jubata* may not be able to tolerate high summertime temperatures common in interior regions of the state (mean daily maximum temperature in Sacramento, CA, in July is 34°C).

DiTomaso et al. (1999) and Lambrinos (2001) determined that *C. selloana* is the dominant *Cortaderia* species along the California coastline south of Santa Barbara County. The southern coast has less fog and higher temperatures (mean daily maximum in San Diego is 27°C) than the central and north coast of California. In northern California, typical coastal temperatures in the summer are close to the optimal temperature for both species (mean daily maximum in Monterey in July is 20°C), and in these areas both species co-occur.

The distribution pattern of both species may also be related to frost tolerance. Although no studies have compared the survival of either species at extremely low temperatures, Costas-Lippmann (1976) observed that an unusual, prolonged frost in Berkeley, CA, severely injured adult *C. jubata* plants, (although they were not killed) but did not harm *C. selloana* adults. Frost is relatively uncommon in coastal California but does occur regularly in the

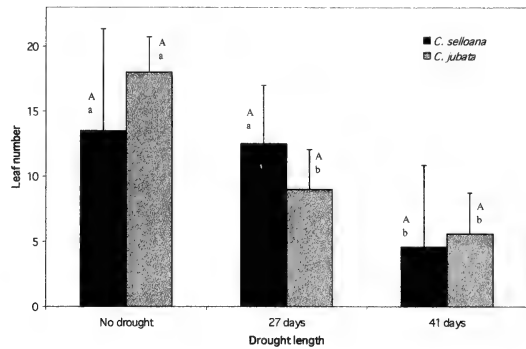


FIG. 5. Effect of extended drought on leaf number in *C. selloana* and *C. jubata*. Bars represent standard deviation. Upper case letters differing within each treatment represent significant difference ($P < 0.05$) between the two species. Lower case letter differing among treatments represent significant differences within a species.

interior regions of the state. For example, coastal Monterey County averages only two frost days per year, while Sacramento experiences an average of 18 frost days per year (<http://www.weatherbase.com/weather/city.php3?c=US&s=CA&refer=>).

Maximum growth of many plant species occurs at full light intensity and growth rates decrease as irradiance is reduced (Radosevich et al. 1997). Morphological responses to decreased light intensity can include reduced tillering, decreased root growth, and lower relative growth rates (Patterson 1985). Low light conditions significantly reduced plant weight, leaf area, and NAR in both *Cortaderia* species. Other studies have documented similar responses to shade in grass species including *Sorghum halepense* (McWhorter 1976), *Rottboellia exaltata* (Patterson 1979), and *Imperata cylindrica* (Patterson 1980). Seedling response in the two species growing with 70 or 85% light reduction were

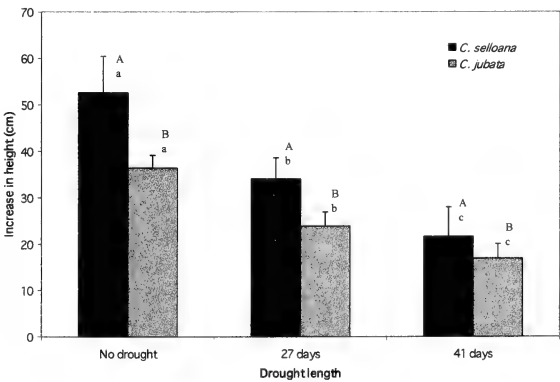


FIG. 6. Effect of extended drought on plant height in *C. selloana* and *C. jubata*. Bars represent standard deviation. Upper case letters differing within each treatment represent significant difference ($P < 0.05$) between the two species. Lower case letter differing among treatments represent significant differences within a species.

TABLE 4. EFFECT OF SOIL MOISTURE ON MEAN PLANT GROWTH OF *C. JUBATA* AND *C. SELLOANA* AFTER 8 WEEKS AT FOUR CONTAINER WATER CAPACITIES. Each data point represents the mean of 12 replicates. * Within each column, different letters indicate a significant difference ($P \leq 0.05$) among water treatments within a species according to Scheffe's multiple comparison test. Bolded and italicized values indicate significant difference ($P < 0.05$) between the two species.

| Species | Percent container water capacity | Height (cm) | Leaf area (cm ²) | Total dry wt (g) | RGR (mg g ⁻¹ day ⁻¹) |
|--------------------|----------------------------------|--------------|------------------------------|------------------|---|
| <i>C. jubata</i> | 25 | 37 b* | 14 c | 0.43 b | 5.4 b |
| | 50 | 61 a | 61 b | 1.25 a | 11.3 a |
| | 75 | 64 a | 103 a | 1.43 a | 12.9 a |
| | 100 | 63 a | 104 a | 1.24 a | 11.0 a |
| <i>C. selloana</i> | 25 | 58 b | 27 c | 0.61 b | 6.8 b |
| | 50 | 74 ab | 84 b | 1.71 a | 14.1 a |
| | 75 | 80 a | 117 a | 1.61 a | 13.5 a |
| | 100 | 81 a | 127 a | 1.75 a | 14.1 a |

nearly identical, with the exception of plant height. Although growth rates were similar in low light, *C. selloana* appears to have an advantage over *C. jubata* in closed canopies because it grows taller, enabling seedlings to grow through existing vegetation sooner to capture more light. The greater size of *C. selloana* may also facilitate encroachment into undisturbed areas.

High growth rates and biomass production of *C. selloana* seedlings under high light conditions can also contribute to the success of *C. selloana* as an ornamental in inland areas. *Cortaderia selloana* seedlings in the greenhouse did not reach a light saturation point, indicating that plants are able to utilize the higher light conditions typical of warm, sunny inland regions of California. In contrast, *C. jubata* apparently reaches maximal growth in moderate light intensities ($960 \mu\text{mol m}^{-2} \text{s}^{-1}$) that are more typical in coastal regions with frequent fog and cloud cover.

Although moisture does not appear to be a limiting factor for either species in coastal regions, water availability may restrict *C. selloana* distribution in hot dry climates. With the exception of dense urban areas like the San Francisco Bay Area, where the two species co-occur, coastal infestations in northern California are primarily *C. jubata*, while *Cortaderia* infestations south of Santa Barbara are generally dominated by *C. selloana*.

Lambrinos (2002) suggested that *C. selloana* has a greater ability than *C. jubata* to use available water. He transplanted seedlings in the field between various plant community types and found no growth differences between the species except in seasonal wetlands, where *C. selloana* seedlings had greater leaf area and survivorship. In this moisture experiment, leaf area was also the most sensitive growth parameter to changes in moisture level. In both species, leaf area was reduced when field capacity dropped below 50%, but plant height and dry weight were not reduced until field capacity was less than 25%. In our experiment, average leaf area dropped by 41% in *C. jubata* and 32% in

C. selloana when moisture content dropped from 75% to 50%.

More vigorous root development in *C. selloana* seedlings growing with high light intensity may account for its ability to more effectively capture water and nutrient resources than *C. jubata*. Under high light conditions in the greenhouse ($960 \mu\text{mol m}^{-2} \text{s}^{-1}$), *C. selloana* did not reach light saturation. With the majority of plant biomass stored in the roots, high growth rates would enable *C. selloana* roots to use up available water more quickly. This may explain why *C. selloana* is restricted to areas with plentiful water in inland areas, such as riparian zones and wetlands. Moisture likely becomes the limiting factor to plant growth when both light and temperature are high in the summer. However, results from this experiment suggest that under moderate temperature and light conditions, like those of the foggy northern California coast, moisture is not a limiting factor.

Although these experiments suggest that the distribution patterns of both *Cortaderia* species in California is based on physiological and morphological factors, it is also plausible that the distribution patterns of both species are related to differences in introduction patterns. It is possible that both species have not yet reached their potential distributions within the state, and their current distribution is based on human dispersal factors, primarily associated with the nursery trade. Although unlikely, it is possible that over a longer time period, both species may co-occur throughout the coast as well as in interior ecosystems. This, however, is more difficult to determine with *C. jubata*, since its history of introduction is not as well documented as that of *C. selloana*.

It is possible that the greater genetic diversity and observed ecotypic plasticity in *C. selloana* is the result of repeated horticultural introductions. Multiple introductions may substantially accelerate the spread of invasive plants from horticultural origin (Reichard and Hamilton 1997). Humans can disperse plants long distances throughout California

and adjacent states, generating multiple foci for spread. Imported horticultural material supplies genetic inputs and may introduce more adaptive traits or higher fertility cultivars. Continued sale and distribution of both male and female forms of *C. selloana* may increase the threat of spread through enhanced reproductive output.

Based on these result, detection efforts should focus on *C. selloana* in more inland, particularly riparian areas and wetlands, environments. Should new invasions be detected in these areas, the highest priority should be given to populations consisting of both functionally male and female plants. Preventing further expansion of newly established populations will depend upon rapid response prior to viable seed development.

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ARCTOSTAPHYLOS GABILANENSIS (ERICACEAE), A NEWLY DESCRIBED
AURICULATE-LEAVED MANZANITA FROM THE GABILAN
MOUNTAINS, CALIFORNIA

V. THOMAS PARKER¹ AND MICHAEL C. VASEY

Department of Biology, San Francisco State University, 1600 Holloway Ave.,
San Francisco, CA 94132

ABSTRACT

Arctostaphylos gabilanensis V. T. Parker and M. C. Vasey is a newly described diploid manzanita species from the Gabilan Mountains in San Benito and Monterey counties, CA. This species demonstrates characteristics that suggest a hybrid origin, with auriculate leaves similar to many maritime species, but also with inflorescence characters including large globose fruits and fused nutlets that indicate a relationship to *A. glauca*. Plants are restricted to soils of granitic origin between 300–700 m from just SE of Fremont Peak, south to near the northern boundary of the Pinnacles. We also provide a key to the northern auriculate-leaved *Arctostaphylos* species of the San Francisco Bay and Monterey Bay regions.

Key Words: Ericaceae, Arbutioideae, *Arctostaphylos*, Gabilan Mountains, diploid hybrid speciation.

In the early 1990's, two botanists independently collected a new manzanita species from the Gabilan Mountains, along the borders of San Benito and Monterey counties, California. Dean Taylor was surveying the area around Gloria Valley in the central Gabilan Mountains and came across a small population of a species he could not determine. Around the same time, Vern Yadon was collecting plants in an area southeast of Fremont Peak in the northern Gabilan Mountains and found a population of manzanitas with which he was not familiar. But it was not until early 2002 that both botanists encountered us at talks and workshops on manzanitas and mentioned their collections. Knowing of no auriculate-leaved species in the Gabilan Mountains, we spent the next year investigating, making collections of both populations and surveying other areas.

In this paper we describe *A. gabilanensis* and its distribution. Additionally, we provide a key for determining auriculate-leaved manzanitas of the northern central coast ranges. We follow Hickman (1993) for the nomenclature of all other species.

SPECIES TREATMENT

Arctostaphylos gabilanensis V. T. Parker and M. C. Vasey, sp. nov. (Fig. 1). TYPE: USA, California, San Benito County, granitic ridge SE of Fremont Peak, above Pescadero Creek, 22 July 2002, V. T. Parker and M. C. Vasey 1087. (Holotype, CAS, Isotype, JEPS).

Frutices erecti vel arborescentes, 1–5 m alti; lignotuber absens; ramorum cortex levis, ruber; ramuli pubescentes, glandulis sessilibus inter trichomes; folia viridi-grisea, ovata, 15–35 mm longa, 11–24 mm lata, \pm sessilia, petiolis interdum 1–4 mm lon-

gis, basis auriculata, apex obtusus, interdum apiculatus, lamina canescens, stomatum numerus parilis utrinque; inflorescentiae nascentes pendulae, paniculatae, ramuli 1–4, pubescentes, glandulis sessilibus inter trichomes, bractea basalis foliacea, 6–8 mm longa, bractae floralae succulentae, subulatae, 2–4 mm longae; corolla alba vel roseo-alba, urceolata vel conoidea, 6–8 mm longa; ovarium canescens; drupa globosa, glabra, rufa-badia, 10–15 mm diametro, mesocarpium obscurum ubi maturum, endocarpium singulare 6–8 semina continens.

Erect shrub or small tree, 1–5 m high, main stem without burl; branches covered by thin medium- to dark-red bark, branchlets pubescent, small, sessile glands present among hairs; leaves gray-green, ovate, 15–35 mm long, 11–24 mm wide, \pm sessile, petioles 1–4 mm long, base auriculate, apex obtuse, sometimes with small tip, blade canescent, stomatal density similar on both leaf surfaces; inflorescence erect to pendent when immature, paniculate with 1–4 branches, glandular pubescent, basal bract leaf-like, 6–8 mm long, floral bracts fleshy, awl-shaped, appearing concave when fresh, 3–4 mm long, spreading, generally glandular pubescent; pedicels usually pubescent but sometimes glandular pubescent or glabrous, 5–10 mm long, corolla white, sometimes tinged with pink, usually urceolate but sometimes conical, 6–8 mm long, ovary usually canescent; fruit a globose drupe, 10–15 mm in diameter, glabrous, red-brown, mesocarp obscure at maturity, seeds usually 6–8, contained within single hard endocarp.

This species is variable in a few characters; most leaves have a fine canescent layer, sometimes with small glands sitting on the surface, especially around the petiole, however, all leaves lose some or all of their pubescence as they age. While stems and rachises are consistently pubescent with sessile glands distributed between the hairs, the pedicels are more variable, usually pubescent, sometimes

¹ Author for correspondence, e-mail: parker@sfsu.edu

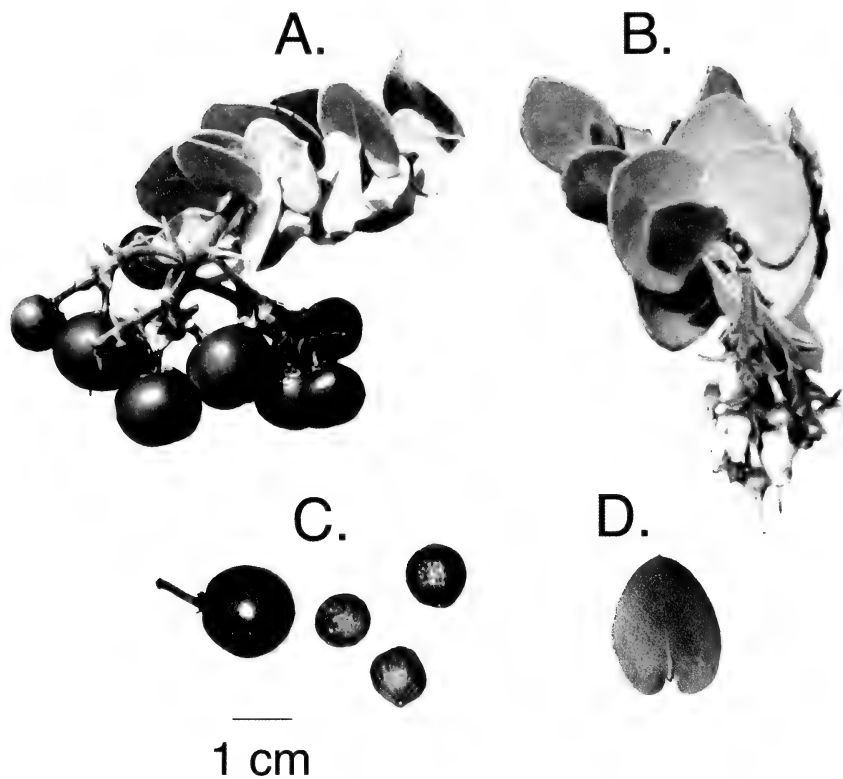


FIG. 1. *Arctostaphylos gabilanensis*. A). Branchlet in fruit; B). Branchlet in flower; C). Fruit and several nutlets; D). Leaf in silhouette.

with sparse glands associated with the hairs or essentially glabrous, especially in the southern population. Most individuals have pubescent ovaries, and as ovaries mature to fruit the hair is lost and the fruit coat is smooth; a few individuals appear to lack pubescence on the ovaries. Generally, the southern population appears less glandular than the northern.

Ploidy level. Immature flowers just beginning to swell were collected from the northern population on 13 January 2003 and preserved in Carnoy’s solution. Later, Kristina Schierenbeck (CSU Chico) and Greg Wahlert (SFSU) determined that *A. gabilanensis* is a diploid with $n = 13$ based upon counts of chromosomes from several individuals.

Distribution and habit. *Arctostaphylos gabilanensis* is found between 300–700 m, restricted to granitic derived soils in the Gabilan Mountains from near Fremont Peak in the north, south to an area near Gloria Valley north of the Pinnacles. Two populations are known. The southernmost is small with less than 30 individuals (near Gloria Valley) while the northern population is extensive, sparsely covering an area of approximately 1000 ha. The northern population is found SE of Fremont Peak, generally confined to a single extensive ridgeline north of and surrounded on three sides by the beginning stretches of Pescadero Creek.

The southern population is found in chaparral dominated almost exclusively by *Adenostoma fasciculatum*. One individual of *A. glauca* is within the population; many populations of *A. glauca* are also found to the east of *A. gabilanensis* and throughout much of the interior areas of the central and southern Gabilans. If other localities exist in the range between the known southern and northern populations of *A. gabilanensis*, *A. glauca* and *A. gabilanensis* may share other sympatric sites.

The northern population is found in a rich chaparral-pine woodland dominated by *A. gabilanensis*, *A. tomentosa* subsp. *crustacea*, *Adenostoma fasciculatum*, *Quercus wislizenii*, *Garrya elliptica*, and *Ceanothus papillosus*. Species of note include a disjunct population of *Vaccinium ovatum* (V. Yadon personal communication) and an extensive population of *Salvia sonomensis*. *Pinus coulteri* occurs scattered and prominent throughout the site.

Other *Arctostaphylos* species besides *A. gabilanensis* and *A. glauca* found in the Gabilan Mountains include *A. tomentosa* subsp. *crustacea* (usually on slopes facing the Salinas Valley), *A. pungens* (volcanic soils in the southern Gabilans) and occasional *A. glandulosa*. Of these species, *A. gabilanensis* appears to share some characters with only *A. glauca*. Auriculate-leaved species were not known previously from the Gabilan range, although we also found a small disjunct population of

A. pajaroensis west across Pescadero Creek from the northern population of *A. gabilanensis* on a ridge adjacent to the Salinas Valley, approximately 20 km from the nearest previously known population. This represents a range extension of *A. pajaroensis* into San Benito County. Other auriculate-leaved species in the region include *A. auriculata* (Mt. Diablo) and *A. pallida* (Oakland and Berkeley hills) to the northeast; *A. imbricata* (San Bruno Mt), *A. montaraensis* (San Bruno and Montara Mts), *A. regismontana* (King's Mt region), *A. glutinosa* (s. Santa Cruz Mts), and *A. andersonii* (s. Santa Cruz Mts) in the Santa Cruz Mountains; *A. pajaroensis* is found to the northwest of the Gabilan Mts in the Pajaro Hills while to the southwest is *A. hooveri* in the northern Santa Lucia Mountains. Of these species, *A. gabilanensis* shares more morphological characteristics like leaf shape and pubescence patterns with *A. auriculata* and *A. glutinosa* than with the others.

Taxonomic relationships. While conjectural, *A. gabilanensis* appears to be of diploid hybrid origin combining characters from an auriculate-leaved species with those of *A. glauca*. The vegetative morphological characteristics indicate genetic origins from an auriculate-leaved species of *Arctostaphylos*, which are generally restricted to foggy and maritime conditions. Of the dozen auriculate species that occur from the San Francisco Bay Area south toward San Luis Obispo, *A. gabilanensis* does not resemble nearby species like *A. pajaroensis* in vegetative characters. Instead, *A. gabilanensis* seems to share more characters with species like *A. glutinosa* (approximately 70 aerial km away), *A. auriculata* (approx. 125 km), and *A. luciana* (approx. 150 km). These three species exhibit a glaucous-gray waxy layer on leaves covered early with short white downy hairs that may thin later as in *A. gabilanensis*. Both *A. auriculata* and *A. luciana* lack glands of any sort on branchlets, while *A. gabilanensis* is sparsely glandular on the branchlets with short or sessile glands and *A. glutinosa* is glandular-hispid or glandular-setose. None of these auriculate-leaved species from central California share reproductive characters with *A. gabilanensis* (Table 1).

Reproductive characters such as the bracts of the inflorescence of *A. gabilanensis*, the large globose fruit and the fused nutlets suggest a relationship with *A. glauca*, a wide-ranging species of relatively hotter and more arid sites in the inner coast range from Mt. Diablo south to Baja California. *Arctostaphylos glauca* is similar in morphology for inflorescence characters and differs only in the fruit surface being viscid; leaf shape and leaf and stem pubescence clearly differs between these two species. *Arctostaphylos gabilanensis* also resembles *A. refugioensis* from the Santa Ynez Mts of Santa Barbara Co. in general appearance and in fruit characters. Gankin (1967) hypothesized *Arctostaphylos refugioensis* also is of hybrid origin between *A. glauca* and an

TABLE 1. COMPARISON OF SELECTED CHARACTERS AMONG SOME CENTRAL CALIFORNIA AURICULATE-LEAVED ARCTOSTAPHYLOS SPECIES. 'Leaf stomata' refer to whether stomata are on both surfaces or only the lower leaf surface. 'Bark' refers to whether the lower stems have a smooth, reddish bark or a rough or shreddy, usually grayish bark. 'Glands on branchlets' indicates whether glands occur on branchlets, and if so, where they occur. 'Fruit' are found either as depressed globose or globose, while 'nutlets' are used to refer to the hardened endocarp covering of the seed, and whether they are separable or fused into a single structure.

| | Leaf stomata | Bark of lower stems | Glands on branchlets | Fruit shape | Fruit diam mm | Nutlets | Fruit surface |
|------------------------|--------------|---------------------|----------------------|-------------|---------------|-----------|------------------|
| <i>A. andersonii</i> | lower | smooth | hispid-setose | depressed | 6-8 | separable | glandular-viscid |
| <i>A. auriculata</i> | both | smooth | none | depressed | 5-10 | separable | pubescent-smooth |
| <i>A. gabilanensis</i> | both | smooth | sessile | globose | 10-15 | fused | glabrous |
| <i>A. glutinosa</i> | both | smooth | hispid-setose | depressed | 7-14 | separable | glandular-viscid |
| <i>A. hooveri</i> | both | smooth | hispid-setose | depressed | 10-15 | separable | glandular-viscid |
| <i>A. imbricata</i> | both | smooth | hispid-setose | depressed | 6-7 | separable | glandular-viscid |
| <i>A. luciana</i> | both | smooth | none | depressed | 6-12 | separable | glabrous |
| <i>A. montaraensis</i> | both | smooth | hispid-setose | depressed | 6-7 | separable | glandular-viscid |
| <i>A. pajaroensis</i> | lower | rough-shreddy | none | depressed | 6-8 | separable | pubescent-smooth |
| <i>A. pallida</i> | both | smooth | none | depressed | 8-10 | separable | glandular-viscid |
| <i>A. regismontana</i> | both | smooth | hispid-setose | depressed | 6-8 | separable | glandular-viscid |
| <i>A. refugioensis</i> | both | smooth | hispid-setose | globose | 10-15 | fused | glabrous |

auriculate-leaved species; *A. refugioensis* is the only other auriculate-leaved species that has a large (10–15 mm), globose fruit with fused nutlets. These two species differ in a number of other characters, for example *A. gabilanensis* has short canescent-style pubescence with sessile glands beneath while *A. refugioensis* is densely hispid or hispidulous with glands on the tips of these long hairs. *Arctostaphylos refugioensis* shares with *A. glauca* a very smooth surface on the fused nutlets, while *A. gabilanensis* is more variable, with nutlets slightly rugulose. The nutlet surfaces of two other species with fused nutlets, *A. rainbowensis* and *A. parryana* ssp. *tumescens*, are similar to that of *A. gabilanensis* in the specimens from our collection.

Many species within *Arctostaphylos* are proposed to be of diploid hybrid origin and these are often narrowly distributed and restricted to a specific soil type or climatic condition (e.g., Howell 1952; Gankin 1966, 1967; Wells 2000). Recent studies (Rieseberg 1997; Rieseberg and Carney 1998) suggest that species of hybrid origin provide successful means of adapting to new habitat conditions, a process known as reticulate evolution.

This newly described manzanita species may well represent an example of this process. *Arctostaphylos gabilanensis* is found in areas that receive muted fog influences. The presence of this combination of maritime fog- and inner coast range-influenced characteristics in *A. gabilanensis* supports models of adaptation to an intermediate habitat (Anderson 1948; Anderson and Stebbins 1954) and indicates a steep environmental gradient in the Gabilan Mountains that may be a natural laboratory for ecological adaptation on a small spatial scale. Much of the Gabilan Mountains are relatively unexplored by botanists compared to other parts of coastal California. While known better for its striking volcanic Pinnacles, the granitic habitats of the Gabilan range deserve more attention from specialists of all types.

Special status consideration. As far as we have been able to determine, *Arctostaphylos gabilanensis* is restricted to two populations, both of which are narrowly distributed. Because of its restricted distribution and the small number of individuals, particularly in the southern population, we recommend that a special status for conservation purposes be considered.

KEY TO AURICULATE-LEAVED MANZANITAS OF THE SF BAY AND MONTEREY BAY REGIONS

- 1. Stomata only on lower leaf surface
 - 2. Stems smooth red, large shrubs of forest edges, S. Santa Cruz Mts *A. andersonii*
 - 2'. Stems rough, gray shreddy barked, sandy soils, Pajaro Hills *A. pajaroensis*
- 1'. Stomata on both leaf surfaces.
 - 3. Fruit globose (10–15 mm diam.), nutlets fused, granitic soils, Gabilan Mts. *A. gabilanensis*
 - 3'. Fruit depressed globose (6–14 mm diam.), nutlets separable
 - 4. Stems lacking glands
 - 5. Fruit glandular-hispid, chaparral, Berkeley-Oakland Hills *A. pallida*
 - 5'. Fruit smooth to sparsely pubescent, lacking glands, Mt. Diablo *A. auriculata*
 - 4'. Stems glandular-hispidulous to glandular-setose
 - 6. Leaves essentially glabrous
 - 7. Plants relatively prostrate or mounding, < 0.5 m, San Bruno Mt. *A. imbricata*
 - 7'. Plants shrubs to small trees, > 0.5 m, San Bruno & Montara Mts. *A. montaraensis*
 - 6. Leaves with some pubescence
 - 8. Leaves curving upward towards tip, boat-like, light-green, dull, glandular-hispid 3–6 cm length, central Santa Cruz Mts (King's Mt and Montara Mt) *A. regismontana*
 - 8'. Leaves flat, grey-green, canescent to sparsely so, Monterey shale, southern Santa Cruz Mts. *A. glutinosa*

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THE DISTRIBUTION AND ECOLOGY OF *TEXOSPORIUM* IN SOUTHERN CALIFORNIA

RICHARD E. RIEFNER, JR.

5 Timbre, Rancho Santa Margarita, CA 92688
riefner@earthlink.net

ROGER ROSENTERER

Department of the Interior, Bureau of Land Management,
1387 South Vinnell Way, Boise, ID 83709

ABSTRACT

New populations and range extensions of *Texosporium sancti-jacobi* are reported from southern California, which include the first known record of the species from Ventura County. The preferred habitat of *Texosporium* is the mosaic of bare-soil patches associated with undisturbed open shrublands that are sparsely vegetated with native forbs, are free of exotic weeds, and support a well-developed biological soil crust. These “open-habitat soils” must become a focus of conservation activities if *Texosporium*, other rare crust organisms, small native annual dicots, and many insects are to persist in southern California.

Texosporium sancti-jacobi (Tuck.) Nád. (woven spore lichen) is a rare lichen that forms inconspicuous white to grayish crusts on soil, organic matter including old rabbit pellets, small twigs in soil duff, and decaying bunch grass stubble (McCune and Rosentreter 1992), basal stems of *Selaginella*, and on other lichens. *Texosporium* is a monotypic genus. It is the only known lichen that produces spores with a thick coat that is analogous to the protective coverings that have evolved in the seed plants (McCune and Rosentreter 1992), which makes it valuable for the study of evolutionary processes (Tibell and van Hofsten 1968). *Texosporium* is endemic to western North America. It is known from only a few extremely small and localized populations from southern Idaho, central Oregon (north of Bend, OR), Benton and Klickitat counties in south-central Washington, and central and southern California (Ponzetti 1999). *Texosporium* (cited as *Cypkelium sancti-jacobi* [Tuck.] Zahlbr.) has been reported from Mexico (Imshaug 1956), but has not been confirmed. These sites are all in open habitats with arid climates.

Texosporium is listed as critically endangered globally by the International Association of Lichenologists (Thor 1996). Additionally, it is an Idaho Native Plant Society Priority 1 Species (Idaho Native Plant Society 1991), is critically imperiled in Oregon (Oregon Natural Heritage Program 2001), is considered threatened by the California Department of Fish and Game (2003), and has been proposed for rare status by the California Lichen Society (Magney 1999).

Until recently, *Texosporium* was known from only a few locations in California, the historic type locality in San Diego County reported by Tuckerman in 1883 and the Pinnacles National Monument in central California (McCune and Rosentreter

1992); and in the southern part of the State from the Aliso Canyon/Cuyama Valley area of Santa Barbara County, on San Clemente Island and Santa Catalina Island, in the San Diego area from San Clemente Canyon (Bratt 2002), and western Riverside County (Riefner et al. 2002). Expanding urbanization has likely extirpated most San Diego County populations, including Kearny Mesa (Magney 1999; Bratt 2002), but remnants of historical populations may be extant (Ponzetti 1999).

SPECIMENS SEEN

Texosporium sancti-jacobi (Tuck.) Nád. (Ascomycetes, Caliciales)—Riverside Co., Gavilan Hills, Hartford Springs Park, UTM 11 0466937E 3741002N (NAD 83), rare on old twigs in soil duff and on rabbit dung on decomposed granitic soils, chamise chaparral, 588 m (1929'), 12 December 2002, Riefner 02-516 (WIS); S of Sage, Wilson Valley, Sage Road N of Wilson Valley Road, UTM 11 0506287E 3715779N (NAD 83), rare on soil with biological crust organisms, chamise chaparral, 707 m (2320'), 12 December 2002, Riefner 02-523 (WIS); San Diego Co., La Jolla, end of Town Center Drive off Eastgate Mall Road, E of I-5 Freeway, UTM 11 0479625E 3638675N (NAD 83), rare on soil with biological crust organisms and on old twigs in soil duff, coastal sage scrub, 111 m (363') Rosentreter 14,612 (Herb. Rosentreter); Kearny Mesa, near San Diego Spectrum Mall off Clairemont Mesa Road, UTM 11 0488208E 3631916N (NAD 27), rare on soil with *Selaginella cinerascens* Maxon and bryophytes and on rabbit dung, remnant mima mound—vernal pool topography, 122 m (400'), 16 December 2001, Riefner 01-778 (ASU); S of Soledad Canyon, E of I-5 Freeway, W side of 805-Freeway off Eastgate Mall Road, UTM 11 0480739E 3638316N (NAD 27), rare on soil with

Selaginella cinerascens and on rabbit dung, chaparral, 122 m (400'), 16 December 2001, *Riefner 01-882* (ASU, WIS); Tierrasanta, Mission Trails Regional Park, E end of Clairemont Mesa Road, UTM 11 0493884E 3632573N (NAD 27), rare on rabbit dung over *Selaginella cinerascens*, chaparral, 244 m (800'), 22 February 2003, *Riefner 03-108* (Herb. Rosentreter, UCR); Shepherd Canyon, Mission Trails Regional Park, UTM 11 0493290E 3633240N (NAD 27), rare on rabbit dung over *Selaginella cinerascens* near vernal pool, coastal sage scrub, 251 m (825'), 22 February 2003, *Riefner 03-109* (ASU, UCR); Mission Gorge near Cowles Mountain County Park, UTM 11 0497495E 3630676N (NAD 83), rare on rabbit dung and twigs in soil duff, chamise chaparral, 333 m (1091'), 22 February 2003, *Riefner 03-122* (WIS); Del Mar, N of Torrey Pines State Park near Del Mar High School, Del Mar Scenic Pkwy., UTM 11 0476538E 3644799N (NAD 27), rare on rabbit dung among ironstone concretions and forbs, chamise chaparral, 114 m (375'), 8 September 2002, *Riefner 02-219* (Herb. Rosentreter, UCR, WIS); Del Mar, Crest Canyon Preserve, Durango Road, UTM 11 0476394E 3644796N (NAD 27), rare on old twigs in soil duff, chamise chaparral (385'), 28 July 2002, *Riefner 02-114* (Herb. Rosentreter, ASU); La Jolla, W of I-5 Freeway, S of Genesee Road and John Jay Hopkins Drive at UC San Diego open space park, UTM 11 0478576E 3637666N (NAD 83), rare on rabbit dung and old twigs in soil duff, chamise chaparral, 121 m (396'), 28 July 2002, *Riefner 02-117* (Herb. Rosentreter, ASU); Soledad Canyon, N of New Miramar Road and W off Eastgate Drive, E of I-805 Freeway, UTM 11 0481610E 3638680N (NAD 83), rare on soil with *Selaginella cinerascens* and bryophytes, mixed chaparral, 109 m (358'), 1 March 2003, *Riefner 03-56* (Herb. Rosentreter, ASU, UCR, WIS); Del Mar, Del Mar Mesa, N side of Los Peñasquitos Canyon at power line right-of-way, UTM 11 0482931E 3643885N (NAD 83), rare on twigs in soil duff and on rabbit dung, chamise chaparral, 129 m (423'), 19 April 2003, *Riefner 03-217* (ASU, WIS); La Jolla, N of end of Town Center Drive off Eastgate Mall Road, E of I-5 Freeway, UTM 11 0479642E 3638975N (NAD 83), locally common on rabbit dung and on old twigs in *Cladonia* and *Selaginella* mats, rare on wood rat dung and on soil, coastal sage scrub, 108 m (353') *Riefner 03-315* (Herb. Rosentreter); Ventura Co., Western Santa Monica Mountains, S of Camarillo, Long Grade Canyon along Portrero Road S of Hueneme Road, UTM 11 0312767E 3781632N (NAD 83), very rare on soil with cryptogamic crust organisms, on rabbit dung, and on old twigs in soil duff with *Selaginella bigelovii*, coastal sage scrub over volcanic rock, 106 m (347'), 29 March 2003, *Riefner 03-207* (Herb. Rosentreter).

In San Diego County, the first author rediscovered two historic populations of uncertain status discussed by Ponzetti (1999); the *Weber & Santes-*

son site on Kearny Mesa (Clairemont Mesa Road near the General Dynamics facility, now the San Diego Spectrum complex), and the *Weber & McCoy* population from clay hills north of Torrey Pines State Park at Del Mar, and we report several populations that are new records for the county (Fig. 1). We also report the first known population of *Texosporium* from Ventura County, and can add two other sites to its known range in western Riverside County. Although widespread, these populations are extremely small localized sites and are susceptible to local extinction owing to changes in land use patterns, expanding urbanization, accelerated erosion, trampling by heavy foot-traffic or crushing by off-road vehicles, and to habitat alterations by fire. Further, the small size of these populations, poor competitive abilities with exotic grasses, and restricted sunny micro-sites within undisturbed open ecosystems, render *Texosporium* highly vulnerable.

In the southern California climate, preferred habitat of *Texosporium* is the mosaic of bare-soil patches and herbaceous-plant dominated micro-sites associated with undisturbed open shrublands. We propose that the term "open-habitat soils" should be used to describe these natural openings or gaps in the arid vegetation that are not maintained by fire. Open-habitat soils are sparsely vegetated with native forbs and scattered bunch grasses, are free of exotic weeds, and support a well-developed biological soil crust. The biological soil crusts help to maintain these open habitats by inhibiting large-seeded exotic plants from germinating (Belnap et al. 2001). The small vascular plant species and cryptogams adapted to these open sites are usually different from those found in disturbance-created open areas in the same region. The open- or clumped-vegetation pattern of many arid systems is often used as a measure of a healthy landscape (Tongway 1994). The presence of biological soil crusts in these open ecosystems can often indicate if the site appears barren but is biologically productive and functioning ecologically, or if the soils are barren, devoid of biological crusts and weedy, and not functioning as an open habitat.

The habitats of *Texosporium* share a number of site-specific characteristics: landforms characteristic of remnant, stable, high-level geomorphic surfaces that support weathered, well-developed soils marked by abrupt argillic (claypan) and cemented silcrete (duripan) horizons or shallow soils over bedrock that restrict deep-rooted plants and promote open environments (Edwards et al. 1970; Knecht 1971; Bowman 1973); a surface layer of well-drained, fine- to coarse-grained soils developed on nearly level terrain; relatively low anthropogenic soil surface disturbance; and physical properties, i.e., duripan soils, cobbles, and shallow depth to bedrock, that restrict bioturbation (the churning of soil by an organism) by fossorial rodents. *Texosporium* and the federally-listed endan-

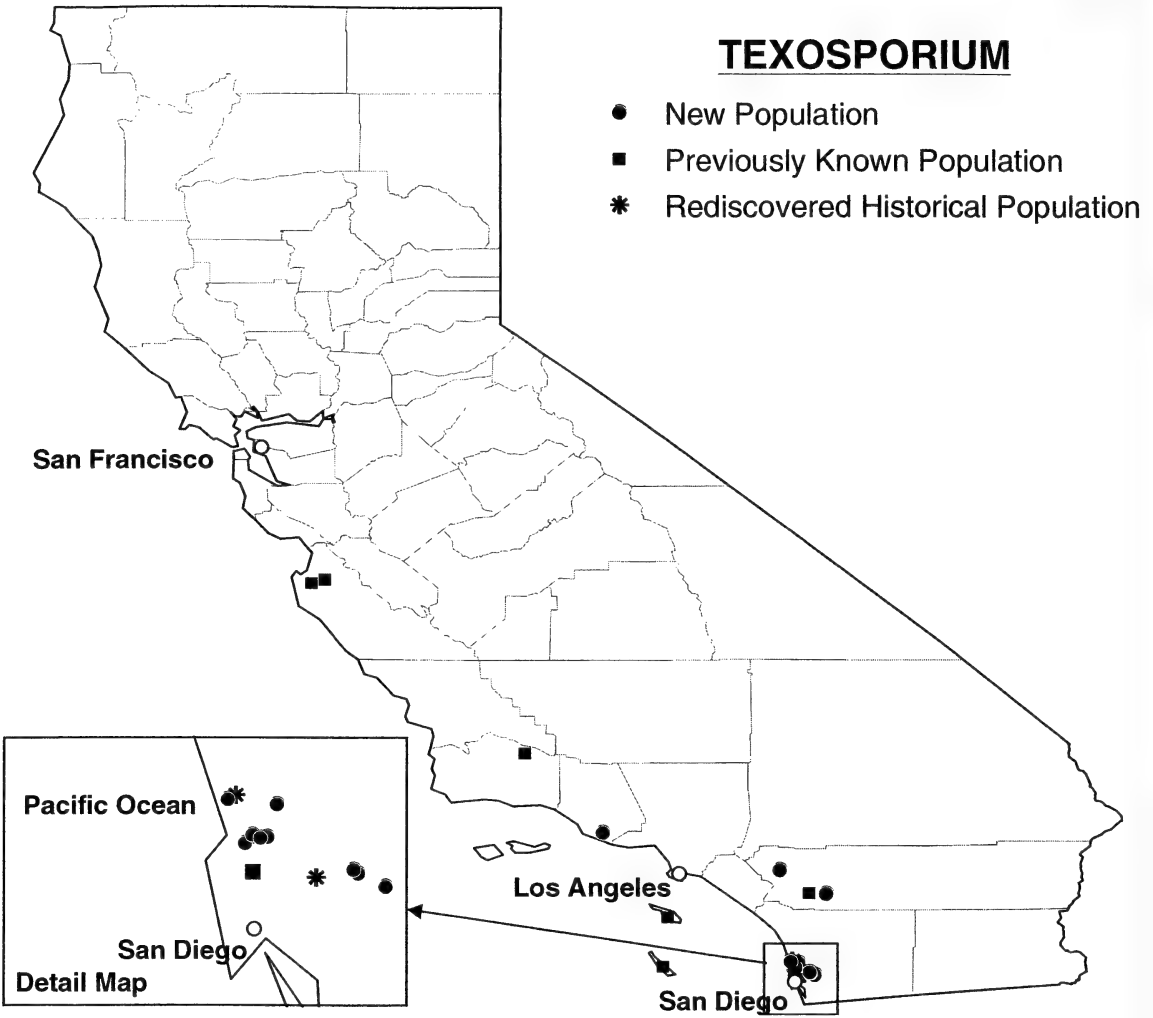


FIG. 1. Known distribution of *Texosporium sancti-jacobi*. Solid circles indicate populations confirmed in the last few years. Squares indicate previously known populations, including two offshore islands, Santa Catalina Island and San Clemente Island. Inset shows the distribution in San Diego County. An asterisk indicates the two historical populations at Del Mar and Kearny Mesa rediscovered during this study. The map was developed from an ESRI base map.

gered quino checkerspot butterfly (“QCB,” *Euphydryas editha quino* [Behr]) share similar open-habitat soils (Riefner et al. 2002), including several currently occupied or historical localities of the butterfly reported by Mattoni et al. (1997). Continuing surveys are warranted for *Texosporium* at other QCB sites, and in similar habitats throughout southern and central California.

Old rabbit pellets are the preferred substrate for *Texosporium* in southern California. On mesas in the coastal fog belt of San Diego County, rabbit pellets with *Texosporium* are often intimately associated with mats of mesa spike-moss (*Selaginella cinerascens*) or crust organisms that stabilize the soil surface and provide open habitats with microclimate conditions that promote rapid surface drying of organic material. The Lindavista Formation underlies many of the San Diego populations. Well-

drained loams with an underlying silcrete duripan, and assemblages of mima mounds and vernal pools are characteristic of the Formation (Bowman 1973). Rabbits have been identified as dispersal vectors of some vascular plants in these landscapes (Zedler and Black 1992), and may play an important role in the dispersal and ecology of *Texosporium*. *Texosporium* spores may be able to pass thru the gut of rabbits unharmed due to their surface ornamentation that mimic a seed coat (McCune and Rosentreter 1992), and may also allow for spore survival in arid habitats.

Accordingly, these interacting components apparently account for the relatively high concentration of *Texosporium* in the San Diego area. Even in the less coastally influenced climate of western Riverside County, the preferred habitat for *Texosporium* are open micro-sites associated with coarse

grus (granitic) substrates that weather to form fine-grained thin argillic (claypan) horizons, which also allow for rapid wetting and drying of organic matter. These soils restrict perennial vascular plant development (Knecht 1971), stabilize decaying organic matter, and provide extensive open habitats with native forbs favorable for rabbits. *Texosporium* is rare in Ventura County on Igneous Rock Land (IrG), which consists of basalt, andesite, and volcanic breccia outcroppings with a thin mantle of relatively stable soil material that is typically barren or has only a sparse brush cover (Edwards et al. 1970). This igneous bedrock is similar to the habitats where *Texosporium* occurs in the drier cold desert of the Great Basin habitats in Idaho and Oregon. In these habitats, the preferred substrate for *Texosporium* appears to switch to larger clumps of organic matter such as dead bunchgrass clumps that are embedded in silty soils. These sites support open shrub communities where the shrubs capture drifting snow and provide protection from drying winds of the desert. *Texosporium* does not occur on rabbit pellets in these Great Basin habitats.

In all known geographic regions, *Texosporium* prefers non-calcareous substrates, fine-textured non-woody organic matter that slowly accumulates on soil in sunny open habitats sparsely vegetated with native plants that have minimal signs of recent disturbance. Most sites are considered late successional or old growth habitats. *Texosporium*, therefore, can be considered an ecologically significant indicator of relatively undisturbed shrub-steppe, grassland, and savanna communities. In all regions *Texosporium* is associated with a well-developed biological soil crust although the specific taxa composing the crusts differ according to region. At the Pinnacles National Monument, and in Santa Barbara County, *Texosporium* is associated with *Aspicillia californica* Rosentreter (Bratt 2002). In western Riverside County and Ventura County, it is intimately associated with another uncommon lichen, *Acarospora thelococcoides* (Nyl.) Zahlbr., which is also a potential indicator of open-habitat soils used by QCB (RER, personal observation). With the exception of the Riverside County localities, *Caloplatea* cf. *subpyraceella* (Nyl.) Zahlbr. shares identical habitats and substrates at all south coast *Texosporium* populations. Bryophytes are also an important component of these habitats, which often include *Asterella californica* (Hampe) Underw., *Bryum argenteum* Hedw., *Didymodon vinealis* (Brid.) Zander, *Funaria hygrometrica* Hedw., *Riccia nigrella* Lam., *R. trichocarpa* Howe, and *Tortula* sp.

Ware (2002) reviewed the ecology of "glades" and pointed out the importance of preserving shallow-soil plant communities in the eastern United States. In California, weathered duripan soils have received conservation attention because of vernal pools. However, upland habitats around vernal pools (Holstein 2001), and other shallow soil and open micro-site habitats that support biological

crusts, and small native annual dicots and invertebrates have been largely ignored. The Endangered Species Act provides an "animal umbrella of protection" that preserves a small number of *Texosporium*'s microhabitats used by QCB in western Riverside County. Because QCB has been extirpated throughout most of its range, many *Texosporium* populations in other counties are not directly linked to this listed species. Accordingly, preservation of undisturbed open-habitat soils must become a focus of conservation activities if *Texosporium* and other rare biological crust organisms, including the liverworts *Geothallus tuberosus* Campb. and *Spaerocarpos drewei* Wigglesw. (CNPS 2001), are to persist in southern California.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

PARNASSIA CIRRATA Piper (SAXIFRAGACEAE). Shasta Co., North Fork of Shotgun Creek, approximately 5.9 km west (280°T) of Sims USFS Fire Station and 4.3 km south (185°T) of Grey Rock Lake, in an area of springs and meadow in rocky serpentine soil. Associated species include *Rhododendron occidentale*, *Darlingtonia californica*, *Chamaecypariss lawsoniana*, *Tofieldia glutinosa*, *Pinus ponderosa*, *Pinus lambertiana*, *Lilium pardalinum*, and *Carex gigas*. Chicken Hawk Hill USGS 7.5' quad, T37N R05W, NE¼ SW¼ Sec 10, UTM 10 547986E 4547788N, elevation 1412 m, 11 Sep 2003, M.J.Lenz (JEPS, CHSC)

Previous knowledge. Although the original description of *P. cirrata* (Piper 1899, Erythea 7(1):128) and early California floras (Jepson 1925, A manual of the flowering plants of California, University of California Press, Berkeley, CA; Munz 1959, A California flora, University of California Press, Berkeley, CA) note it as occurring in the Sacramento River drainage, more recent literature (Hickman 1993, The Jepson manual: higher plants of California, University of California Press, University of California Press, Berkeley, CA; CNPS 2003, California Native Plant Society, Inventory of rare and endangered plants (online edition, v6-3), Rare Plant Scientific Advisory Committee, California Native Plant Society, Sacramento, CA) only mentions its southern California distribution. Piper's description, based on the type specimen from Mt. San Bernardino (Parish #156, 1879), includes a reference to a co-mounted collection by W.H. Brewer (#1445) from the "upper Sacramento River, growing with *Darlingtonia*." Jepson mentioned *P. cirrata* as occurring in the "upper Sacramento River," and Munz noted its distribution in the "upper Sacramento V." However, the Jepson Manual (Hickman 1993) mentions it occurring in only the San Gabriel Mountains, San Bernardino Mountains, and Mexico. Likewise, CNPS (2003) mentions it occurring in San Bernardino and Los Angeles counties. Additionally, the California Department of Fish and Game's California Natural Diversity Database contains no records of *P. cirrata* from the northern part of the state.

Significance. This collection verifies the occurrence of *P. cirrata* in the Sacramento River canyon, as initially described by Piper over 100 years ago. It also raises questions as to whether the northern populations are significantly disjunct from those in southern California, or if *P. cirrata* has perhaps been overlooked at intervening locations. Subsequent to this collection, review of the *P. fimbriata* collections at CHSC determined that two of those collections had been misidentified and were in fact *P. cirrata* (Lawrence Janeway personal communication). One of those collections is from the Trinity River drainage in Trinity County, and the other is from the Scott River drainage in Siskiyou County.

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—MARTIN J. LENZ, 400 Del Monte St., Montague, CA 96064. mjlenz@inreach.com.

COLORADO

EICHHORNIA CRASSIPES (Mart.) Solms (PONTEDERIACEAE).—Weld Co., Epple Park, 43rd Ave. and 4th Street, [Greeley], 40°25'41"N, 104°45'15"W, 25 Sep 2003, J. Grasser 373 (GREE); Weld Co., Elk Lake, located on the corner of 35th Ave and [US] Highway 34, Greeley, 40°23'N, 104°44'W, 22 Sep 2002, R. Wallace 10 (GREE); El Paso Co., Little Turkey Cr. Drainage, in shallow pond growing with *Pistia stratiotes*, *Potamogeton*, and *Typha*, T16S, R67W, S8, 2380 m, 31 Aug 2000, T. Kelso & G. Maentz 00-169 (COCO, COLO); Boulder Co., City of Louisville, Coal Creek Golf Course, floating in shallow water in the middle of Coal Creek, north of Dillon Road and about 300 m east of the golf course clubhouse and parking lot, 25 Sep 2001, W. F. Jennings 1366 (GREE).

Previous knowledge. This species is becoming sporadically established in many states east of the Mississippi River and in Ontario, Canada. West of the Mississippi it is known from Texas, Arizona (where it is a noxious weed), California, and possibly Washington (Kartesz and Meacham 1999, Synthesis of the North American flora, Version 1.0 [compact disc], North Carolina Botanical Garden, Chapel Hill, NC).

Significance. These are the first collections from Colorado. This species and *Pistia stratiotes* (see next note) are commonly used in tropical fish aquaria and may be entering aquatic habitats from unintentional disposal by dealers or aquarium enthusiasts. The collection by Wallace in Weld County was from an artificial cattail marsh on the edge of a strip mall near a pet store. According to the groundskeeper at the golf course in Boulder County, the plants float down the creek from an unknown source. The two to three dozen plants (some in flower) seen by Jennings are only a fraction of what he had seen earlier. It is uncertain whether the species can survive winters, but since some larger bodies of water (e.g., Pueblo Reservoir) on the plains of Colorado sometimes do not freeze over during the winter, it may persist for more than one year.

PISTIA STRATIOTES L. (ARACEAE).—El Paso Co., Little Turkey Cr. Drainage, in shallow pond growing with *Eichhornia*, *Potamogeton*, and *Typha*, T16S, R67W, S8, 2380 m, 31 Aug 2000, T. Kelso & G. Maentz 00-170 (COCO, COLO).

Previous knowledge. This species, commonly called Water Lettuce, is an escapee in several states (CA, AZ, TX, LA, MS, FL, GA, SC, NC, NY) and is reported to be present from Missouri and Ohio (Kartesz and Meacham 1999, Synthesis of the North American flora, Version 1.0 [compact disc], North Carolina Botanical Garden, Chapel Hill, NC).

Significance. First collections in Colorado and the Rocky Mountain region.

PHYSARIA BRASSICOIDES Rydb. (BRASSICACEAE).—Weld Co., Eagle Rock Sanctuary (now defunct) on Eagle Rock Ranch, T11N, R65W, S8, May 1977–Sep 1978, W. E. Harmon 8900 (GREE); Eagle Rock Sanctuary, T11N, R 65W, S15, May–Sep 1977–1978, W. E. Harmon 8911 (GREE).

Previous knowledge. According to the PLANTS Database this species occurs in ND, SD, NE, MT, and WY (<http://plants.usda.gov/cgi-bin/plant-profile.cgi?symbol=PHBR5>). In Wyoming its closest occurrence is in Laramie county (<http://www.esb.utexas.edu/tchumley/wyomap/BRA/phybra.pdf>). The USGS-NPS Vegetation Mapping Program also reports *Physaria brassicoides* from the "Siltstone-Clay Butte Sparse Vegetation" community on the Oligocene aged Brule Formation (<http://biology.usgs.gov/npsveg/scbl/descript/scb.pdf>). An illustration of the species by Debbie McNeil is available from the Montana Natural Heritage Program (<http://nhp.nris.state.mt.us/plants/illustr/sid1365i.pdf>).

Significance. First collections in Colorado. This species is the only member of *Physaria* endemic to the Great Plains (The Great Plains Flora Association, 1986). It is not a common plant, and one of us (Jennings) doubts whether more than 50 sites exist throughout its entire range. *Physaria brassicoides* occurs primarily on sparsely vegetated sites that are frequently steep and eroding. The nearest collections are approximately 100 km north at Scotts Bluff National Monument in Nebraska and the Wyoming counties of Albany, Platte, and Laramie (e.g., Dorn 4975 [COLO]). Colorado collections are from the same geological formation as the type locality in Scotts Bluff. *Physaria brassicoides* can be distinguished from the similar species *Physaria vitulifera* Rydb. by its lack of teeth on the petiole and the obcordate fruits.

We thank Dr. S. Kelso of Colorado College for sharing collection data and to Dr. T. Ranker for permission to use the herbarium at the University of Colorado (COLO). Work supported by NSF grant DBI-0237149.

—N. SNOW, J. BRASHER, R. WALLACE, J. GRASSER, Department of Biological Sciences, University of Northern Colorado, Greeley, CO 80639; and W. F. JENNINGS, P.O. Box 952, Louisville, CO 80027. (N. Snow: Neil.Snow@unco.edu).

COLORADO

ECHINOPS SPHAEROCEPHALUS L. (ASTERACEAE).—Montrose Co., First Park, ca. 3 km east of Nucla, off 30.50 Road, south of town reservoir, 38°15'23"N, 108°30'29"W Nucla Quad T46N R15W sec. 10, 11 August 2000. M.W. Denslow & S. Grother 528 (RSA)

Previous knowledge. *Echinops sphaerocephalus* L. is native to south and central Europe (Chater in Tutin et al. [eds.] 1976, Flora Europaea, Vol. 4. Cambridge University Press, Cambridge, England) and has been collected throughout much of the northeastern United States as well as in California, Colorado, Washington (Kartesz and Meacham 1999, Synthesis of the North American flora, Version 1.0 [compact disc], North Carolina Botanical Garden, Chapel Hill, NC) and Wyoming (Dorn 2001, Vascular plants of Wyoming, 3rd ed., Mountain West Publishing, Cheyenne, WY). In Colorado it is rarely collected and known collections are centered between Denver and Fort Collins.

Significance. This is the first collection of *Echinops sphaerocephalus* L. for the western slope of Colorado. Not mentioned in Weber and Wittman 2001 (Colorado flora: western slope, 3rd ed., University Press of Colorado, Boulder, CO). This collection is approximately 400 km from the nearest vouchered collection in the Denver area.

The population appeared to be reproducing in 2000 and is still present at this site.

—MICHAEL W. DENSLOW, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711, michael.denslow@cgu.edu; and SHEILA GROTH, San Miguel County Weed Manager, Box 130, Norwood, CO 81423.

COLORADO

SCORZONERA LACINIATA L. (ASTERACEAE).—Delta Co., Jumbo Mountain, ca. 6.4 km ENE of Paonia T13S, R91W, S35 W½ & S34 E½, 1830–2230 m (6000–7300 ft), squaw-apple and serviceberry zone and pinyon-juniper slopes above with sandstone and shales, 17 May 1997, R. L. Hartman & Kevin J. Taylor 56318 (RM); ca. 4.8 km NNE of Crawford, T15S, R91W S17, 1830–1980 m (6000–6500 ft), juniper and aspen shrubland (*Atriplex*), 26 May 1997, K. J. Taylor 521. (COLO, RM); Archuleta Co., San Juan River Basin, south of Chimney Rock in the Chimney Rock Archaeological Area, just outside small visitor center building, UTM Zone 13 N4116446, E295290, ca. 2037 m (6680 ft), edge of pavement next to parking lot, under Ponderosa Pines, 9 June 2001, M. W. Denslow & M. J. Lyon 654 (RSA).

Previous knowledge. *Scorzonera laciniata* L. (*Podospermum laciniatum* (L.) DC.) is native to south and central Europe (Chater in Tutin et al. [eds.] 1976, Flora Europaea, vol. 4. Cambridge University Press, Cambridge, England). It was first discovered in North America in 1950 near Boulder, Colorado (Great Plains Flora Association 1986, Flora of the Great Plains, University Press of Kansas, Lawrence KS) and has been collected in eastern Colorado, Kansas, Montana, Nebraska, New Mexico, Texas, and Wyoming (Kartesz and Meacham 1999, Synthesis of the North American flora, Version 1.0 [compact disc], North Carolina Botanical Garden, Chapel Hill, NC).

Significance. These collections represent the first records for the western slope of Colorado. This taxon previously has not been reported in floras or manuals for the western slope of Colorado (Weber and Wittman 2001, Colorado Flora: western slope, 3rd ed., University Press of Colorado, Boulder, CO). Additionally it was not reported for the state by Harrington (1954, Manual of the plants of Colorado, Sage Books, Denver, CO). The collection in Archuleta County is approximately 161 km from the nearest voucher in Delta County, suggesting that the species may be more widespread in western Colorado. Despite this possibility, recent intensive fieldwork with over 43,309 new numbered collections from an area of more than 71,780 km² on the western slope of Colorado by graduate students (floristic M.S. theses in Botany) and staff of the Rocky Mountain Herbarium have failed to encounter it in the Gunnison Basin (K. J. Taylor 2000, A floristic inventory of the Northern Gunnison Basin, Colorado; M. Arnett 2002, A floristic inventory of the Southern Gunnison Basin and the Southeastern Uncompahgre Basin, Colorado), the western San Juans and vicinity (L. M. Moore 1998, Floristics of the Upper Dolores River drainage and adjacent areas, Southwestern Colorado; M. J. Lyon 1996, A floristic survey of the San Miguel and Lower Dolores River drainages Colorado and Utah), or the White River Plateau region (J. P. Vanderhorst 1993, Flora of the Flat Tops, White River Plateau, and vicinity in northwestern Colorado).

—MICHAEL W. DENSLOW, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711, michael.denslow@cgu.edu; and RONALD L. HARTMAN, Rocky Mountain Herbarium, Department of Botany, University of Wyoming, Laramie 82071-3165.

OREGON

CRUPINA VULGARIS Cass. (ASTERACEAE).—Wallowa Co., steep southeast-facing slopes in Joseph Canyon, ca. 1 km SE of Paradise, canyon grasslands in mosaic with shrublands (*Pseudoroegneria spicata*/*Festuca idahoensis* with *Symphoricarpos albus*), 45°55.46'N, 117°12.6'W, 1275 m, 6 May 2003, Roché & Korfhage s.n. (OSC); *Pseudoroegneria spicata* grasslands 1 km east of the old Rimrock Café on Highway 3, 45°53.5'N, 117°15.2'W, 1200 m, 7 May 2003, Roché & Korfhage s.n. (OSC); and a third location on steep south-facing slopes above Jack Lowery Fork of Cache Creek, in the Hells Canyon National Recreation Area, canyon grasslands (*Pseudoroegneria spicata*, *Poa secunda*), rocky silt loam soils, 45°59.3'N, 116°56.8'W, 1090 m, 9 May 2003, Roché & Korfhage s.n. (OSC).

Previous knowledge. *Crupina vulgaris*, native to the Mediterranean region, was first discovered in Wallowa County by Clair Button, BLM botanist, Vale District, on 6 September 1995, but he did not report it or save specimens. His field notes indicated that there were a few plants remaining in flower at the bottom of Joseph Canyon “on a hot, dry, compacted microsite at the edge of a coral” just upstream from the mouth of Rush Creek (45°55.935'N, 117°10.072'W). The next discovery was seven years later in August 2002, by Nez Perce Tribe biologists, Shana Kozusko and Blair McClarin, while doing wildlife surveys on the Precious Lands Wildlife Area in Joseph Canyon (A. Sondenaa, Nez Perce Tribe, Lapwai, personal communication). Later that year it was found on a parcel of land acquired during the summer of 2002 by the Bureau of Land Management in Joseph Canyon (M.

Wood, BLM, Baker City, personal communication). An outlier population discovered by Asotin County rancher Mike Haberman in T6N R45E sect. 27 SE¼ of SE¼ in the summer of 2003 forms the northern boundary of the known infestations in Joseph Canyon (45°57.873'N 117°10.256'W). A third location, in Hells Canyon, was discovered in July 2002 by a Forest Service contractor, Skip Royes, when spraying yellow starthistle with a horse-mounted pack on Jack Lowery Fork of Cache Creek. Following the discovery by the Nez Perce Tribe biologists, Mark Porter, coordinator of weed program for Wallowa Resources began an inventory of potential sites and reported the additional infestations.

Significance. These collections represent the first record of this species from Wallowa County, Oregon. Prior to these discoveries *Crupina vulgaris* was known in Oregon from a single location in Umatilla County, a population that was discovered in 1987. The populations in Joseph and Hells Canyons are most likely not related to the Umatilla site but rather to larger infestations across the Snake River in Idaho. *Crupina vulgaris* was first discovered in western North America in Idaho (Stickney 1972, Madroño 21:402), where it grows on south-facing grasslands in the Clearwater, Snake, and Salmon River canyons. During the first half of the 20th century thousands of sheep were trailed between winter range in Hells Canyon and summer range in the mountains of northern Idaho each year, possibly carrying seeds in the wool. All of the locations in Wallowa County are remote, steep terrain, making it likely that the infestations escaped detection for decades, a scenario consistent with *Crupina* discoveries in other states (Roché et al. 2003, Weed Research 43:177–189). Although decades have elapsed since the weed's long-distance dispersal mechanism ended, additional discoveries of *Crupina vulgaris* in Hells Canyon are probable, given the region's grazing history, limited access, and difficult terrain.

—CINDY T. ROCHE, 109 Meadow View Drive, Phoenix, OR 97535, crupinaqueen@charter.net.

REVIEW

Plant Resins: Chemistry, Evolution, Ecology, Ethnobotany. By JEAN H. LANGENHEIM. 2003. Timber Press, Portland, OR. 586 pp. Hardcover \$49.95. ISBN 0-88192-574-8.

Interactions between plants and animals are largely mediated by chemical products, usually produced by the plants. One such plant product, which has evolved repeatedly throughout the plant kingdom, is resin. Plant resins, and their many uses by people, animals, and the plants themselves, are the subject of a fascinating new book by Jean Langenheim.

Although the definition of natural resin varies, it is generally accepted as a plant secretion that is translucent, often sticky, and soluble in organic solvents rather than water. Resins are generally synthesized and released to defend plants against attack by microbes, insects, or other animals (Langenheim 1969). This function alone involves interactions between many thousands of plant, animal, and microbe species, in virtually every corner of the world. However, the story of plant resins is even more involved, because resins, being chemically distinctive and diverse, are also collected and used by animals, including humans, for a variety of purposes. In turn, some plants have capitalized on animal use of resins by secreting resins to attract animals rather than repel them. These animals are then manipulated to perform needed services (e.g., pollination; Armbruster 1984). Human interest in, and use of, resin has a long history. Resin has even affected popular culture: e.g., amber (fossil resin) is a semi-precious gem, prized in jewelry. The most recent manifestation of popular interest in fossil resin is as a potential source of ancient DNA (e.g., dinosaur DNA in *Jurassic Park*, although this remains clearly in the realm of fiction).

Jean Langenheim has spent much of her professional career studying the chemistry, botany, and ecology of ambers and resins. It is gratifying to see a lifetime of work with a wide cast of collaborators (e.g., Stubblebein and Langenheim 1977; Arrhenius and Langenheim 1983) reviewed authoritatively in one volume. This book is much more; it is the most comprehensive review yet written on all aspects of plant resins, from chemistry and biology to ethnobotany and commerce. The list of topics in the table of contents gives an idea of the range: 1) production of resin by plants (chemistry, biosynthesis, plant taxonomic distribution, evolutionary trends, anatomy, secretion, storage), 2) geological history and ecology (amber, plant-herbivore interactions and plant defense, animal use of resins, resin-based plant-pollinator interactions, physiological roles of resin, ecosystem significance), and 3) ethnobotany

of resins (history of human use in medicine and commerce, modern uses, future uses, and conservation).

This book is obviously a valuable treasure-trove of information about plant resins, plants that secrete them, and animals and microbes that interact with these plants. Anyone working on the ecology or chemistry of ambers, terpenoids, phenolics, or related plant products will want to read this well produced and well-illustrated book and have it handy as a reference.

I was at first uncertain just who, other than specialists, would be interested in such a scholarly, yet wide-ranging book. The book is reasonably easy to read, striking a pleasant balance between being well referenced, with scholarly journal-style citations, yet without the distraction of overly abundant citations. But the text is not entertainingly chatty, nor does it recount the personal excitement of fieldwork and scientific discovery, as might a popular book. So who then, besides a specialist, will be attracted by such a volume? The answer, I suspect, lies in the ethnobotany.

For me, the section on human use of resins was a pleasant excursion into incidental issues I knew rather little about. Upon reflection, however, I now see this section as the most important and compelling part of the book for the broader readership. After all, nearly everyone in western society has seen amber, heard of frankincense and myrrh, smelled incense, and tasted hoppy beer and perhaps even retsina (all of which contain or are resins). The cultural and commercial links of human society to plant resins are far more extensive, varied, and complex than this reader could have imagined. For example, I had no idea that kauri resin (*Agathis australis*, Araucariaceae) was one of New Zealand's main exports for over 100 years, or that this came about as a result of an English boy finding, by accident, some discarded resin floating in the Thames in 1836 (it had been brought to London for analysis but judged to be worthless; McNeill 1991). This fascinating review of the complex history of human use of resins will thus probably be the primary source of attraction for the non-specialist reader (although I hope they will also read and be fascinated by the wealth of natural history in the first half of the book).

In any book of this size (nearly 500 pages of text!), there will always be occasional inconsistencies and things to criticize. For example, on page 38, we read that β -amyrin is a component of resins only in plants in the Burseraceae, but then on page 234 we read that it is an important resin component of some plants in the Euphorbiaceae (yes, I would spot this). A few other minor inconsistencies can

be spotted, but otherwise the book is well edited and remarkably free of errors of fact or typography. There could have been more detail in a few areas. For example, I would have liked to see a little more coverage of animal uses of resin. The material that is presented is fascinating, but it leaves out many components of this area of growing interest. Although conservation is mentioned briefly in the last section of the book, one might wish to have seen the topic explored a little more thoroughly, and perhaps even passionately. Dr. Langenheim has certainly witnessed tremendous changes in tropical landscapes over her years of travel and research. Where plant resins fit into that crisis would have been interesting to explore in a little more detail. And it never hurts to raise these issues in a book that will be read by a cross-section of the voting public. But these are all minor quibbles reflecting my own biases and values.

To summarize, this is an impressive piece of scholarly work. It makes a fascinating book, which is well produced and lavishly illustrated. This is a volume that many chemical ecologists, natural-product chemists, and ethnobotanists

will want to own. I also expect that member of the wider public who are interested in plants and their uses, or in the history of trade in plant products, will appreciate this book.

—SCOTT ARMBRUSTER. School of Biological Sciences, King Henry Building, King Henry I Street, University of Portsmouth, Portsmouth PO1 2DY, UK. Scott.Armbruster@port.ac.uk

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REVIEW

The sunflower forest. By WILLIAM R. JORDAN III. 2003. University of California Press, Berkeley, CA. 256 pp. \$27.50. ISBN 0-520-23320-4.

In *The Sunflower Forest*, Bill Jordan provides a detailed exploration of the idea that restoration can serve as a way for humans to heal their relationship with nature. Jordan has presented the main ideas in this book elsewhere, through his editorials when he was editor of *Ecological Restoration* and a number of book chapters. In this book, he further develops these ideas drawing on a wealth of examples of restoration projects, as well as analogies ranging from Huckleberry Finn to Thoreau to the bible. A recurring theme in the book is the ecological fall of grace of humans through Adam and Eve's being banished from the Garden of Eden and the necessity of resolving this relationship.

Jordan begins the book by presenting his definition of restoration and offering an overview of the diversity of types of ecological restoration projects. He spends the next five chapters on a lengthy exploration of the "shameful" relationship that humans have had with nature. In the latter chapters of the book he extols the importance of restoration in atoning for this flawed human-nature relationship, emphasizing the importance of ritual in this healing process. As an example, Jordan writes (p. 172):

"This is no doubt why the use of fire as a tool for restoring ecological communities . . . has often been controversial, fire being an archetypal emblem of destructive chaos. Yet like the epic floods, murders, and battles of myth, fire can prepare the way for renewal—a resurrection of the kind symbolized by the phoenix or, for the Christian, by the Pentecostal tongues of flame. There is a striking resonance here with classic modes of sacrifice, as Jerry Escher a restorationist in Tacoma, Washington, remarks: like the innocent victim of traditional sacrifice, the weeds and exotic plants the restorationist kills die for our sins. This may be painful, but we remind ourselves, the victim must be innocent because what is involved here is not a punishment for sin, but an acknowledgement of existential shame."

I agree with Jordan that restoration not only helps to conserve species and ecosystems but that restoration can also be an important transformative experience for those who participate. In a number of cases, however, Jordan carries his ideas too far. If a goal of restoration is build societal support, then imposing Christian symbolism will likely burn more bridges than it is meant to build. As an ex-

ample, in his discussion of ritualizing nature, Jordan recounts an example of painting trees that were girdled to prevent them from encroaching a restored prairie; the painting served as a "sacrificial ritual—not only performing the shameful act but intensifying the shame by highlighting it." Moreover, he argues that restoration should develop into a performing art. Jordan (p. 177) in critiquing a Civilian Conservation Corps tree planting effort, says:

"If . . . CCC enrollees had been recruited from local communities, and if the work had been ritualized, with project planners and crew supervisors calling in artists and ritualists, and taking their advice as seriously at that of the scientists and technical experts involved in the work, my guess is that the results would have been very different."

Certainly, restoration requires creativity, and local human community involvement in and support for restoration projects is essential to their success. But, in my opinion, developing restoration as a performing art in itself takes the focus away from the critical importance of basing restoration efforts on sound science.

Despite his overall optimistic view of the power of ecological restoration, in chapter 5 Jordan does recognize that some ecological changes may be irreversible even with restoration. As a restoration ecologist, I think it is essential that we are honest about our ability to restore ecosystems, so restoration does not become a substitute for conservation of less disturbed ecosystems. Jordan suggests that knowing which ecosystems or communities cannot be restored ('ecological Humpty Dumpties') will help us prioritize which ecosystems to conserve. I found this point a bit simplistic, since there are few if any "restored" ecosystems in which all species and functions have been restored successfully.

Restoration ecology is a value-laden process. As I emphasize to students in my Restoration Ecology classes, it is important that we recognize the ethical decisions we are making when we actively modify ecosystems in an effort to restore them. That said, I found it difficult to remain focused on the lengthy philosophical discussions in this book that have been covered more succinctly elsewhere (e.g., Jordan 1994, 2000). For most Madroño readers, I would recommend that they read one these shorter treatises. I should make the caveat that I am an ecologist who chooses to focus my research on learning about ecosystems in order to be able to improve restoration efforts, and not an environmental philosopher. This book may be of more interest

to those who spend more time engaging in philosophical inquiry. This book is definitely thought provoking and is a change from much of the ecological and environmental literature as it ultimately provides an upbeat view of the potential for humans to improve their relationship with nature. Jordan provides a powerful call to action for humans to not throw up our hands in despair over the ever mounting environmental degradation but to put our energy towards working to improve the situation and ourselves.

—KAREN HOLL, Environmental Studies Department,

University of California, Santa Cruz, CA 95064.
kholl@ucsc.edu

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RUPERT BARNEBY AWARD

The New York Botanical Garden is pleased to announce that Karen Redden, currently a graduate student in the Department of Biological Sciences, George Washington University, Washington, D.C., is the recipient of the Rupert Barneby Award for the year 2004. Ms. Redden will be studying the systematics of a diverse group of legumes centered around *Dicymbe*, *Paloue*, *Paloveopsis*, *Heterostemon*, and *Elizabetha* that are concentrated in the Guiana Shield area.

The New York Botanical Garden now invites applications for the Rupert Barneby Award for the year 2005. The award of US \$1,000.00 is to assist researchers to visit The New York Botanical Garden to study the rich collection of Leguminosae. Anyone interested in applying for the award should submit their curriculum vitae, a detailed letter describing the project for which the award is sought, and the names of 2–3 referees. Travel to the NYBG should be planned for sometime in the year 2005. The application should be addressed to Dr. James L. Luteyn, Institute of Systematic Botany, The New York Botanical Garden, 200th Street and Kazimiroff Blvd., Bronx, NY 10458-5126, USA and received no later than December 1, 2004. Announcement of the recipient will be made by December 15th.

Anyone interested in making a contribution to THE RUPERT BARNEBY FUND IN LEGUME SYSTEMATICS, which supports this award, may send their check, payable to The New York Botanical Garden, to Dr. Luteyn.

REVIEW

Atlas of the Vascular Plants of Texas. By B. L. TURNER, HOLLY NICHOLS, GEOFFREY C. DENNY and ODED DORON. 2003. Sida, Botanical Miscellany 24. Botanical Research Institute of Texas, Fort Worth, TX. Vol. 1. Dicots, 1–648 pp. \$50.00. ISBN 1-889878-08-1; Vol. 2. Ferns, Gymnosperms and Monocots, 649–888 pp. \$40.00. ISBN 1-889878-09-X. 2 vol. set. \$80.00.

This is a two-volume atlas of the vascular plants of Texas with the “text” consisting of 5017 dot maps showing the county-level distribution of native and naturalized taxa within the state. The maps, six per page, show outlines of the 254 Texas counties. The taxa are arranged in alphabetical order, by family, genus, and species, with one species shown per map except in some cases where multiple varieties are recognized. The taxon names are given without authorities, and in the case of new names, the synonyms are often, but not consistently, given.

The distribution data were derived from a combination of sources. Primary were the herbarium records from the University of Texas in Austin (TEX-LL) and Sul Ross State University in Alpine (SRSC), but supplementary data were obtained from maps and distribution listings in selected taxonomic monographs, from the *Atlas of the Great Plains* (Great Plains Flora Association 1977) and from selected local, county and state floras, as well from on-line maps from the Flora of Texas Consortium database hosted at Texas A & M. Some data also came from the herbaria at BRIT. Michael Powell of SRSC provided maps of Cactaceae. Taxa from smaller counties usually are indicated by a central dot or multiple dots when several collections are known. In the larger trans-Pecos counties, with multiple collections, dot location indicates relative distribution within the county. In some taxa, additional data are presented from “road trips” that Turner made, these usually being marked by continuous dots across the map. The latter are unvouchered sightings.

The “Atlas” is primarily the work of Billie Turner, long-time student of the Texas Flora. The co-authors were undergraduate and graduate workers who transferred the data to a digital format. Turner reviewed the identification and annotated all Texas specimens at TEX-LL and SRSC and aligned the classification according to his species and infraspecific concepts. Turner’s species concept has been solidified into an eco-geo-morphological model, stating that species may differ in one or more morphological characters, or may be ecologically or geographically differentiated. Thus taxa that consistently differ in some character, large or small, can be considered as distinct species, particularly if

they are also geographically or ecologically distinct. Turner uses subspecies only as a means of clustering varieties. Varieties must be geographic and show introgression in areas of overlap, otherwise the taxa are considered either species or insignificant forms. His concepts result in a distinctive classification, in that what many systematists might consider merely an ecotype, can be considered a distinct species. Also, taxa that differ in some small character, that are often considered varieties by many systematists, can be elevated to species if no introgression is shown for that character. Thus the classification presented in the “Atlas” reflects these concepts.

Most of the species recognized closely follow the alphabetical checklist of Jones et al. (1997) except where Turner’s classification differs. Jones’ book provides adequate synonymy for most taxa, but when the classification differs and no synonyms are given, the reader is left to his own resources to determine the origin of the name. The International Plant Name Index on the Web, however, will give references to new combinations, if they have been published.

The volumes are published by the Botanical Research Institute of Texas (BRIT) in their excellent *Sida-Botanical Miscellany* series that has published various floras, taxonomic monographs, and botanical compendia. The two volumes have strong plastic-coated paperback bindings, are well printed, with clean maps and text, and have a good solid feel to the hand. BRIT is to be lauded for their published contributions to the field of Botany.

In groups that Turner knows well, the nomenclature and distribution data are probably quite accurate. But in other groups there appear to be errors in identification and what I consider to be errors in taxonomic judgment. In the first map I consulted, that of the dioecious *Amaranthus acanthochiton*, I found a much wider distribution than I expected. I then found that 7 of 14 male plants at TEX-LL and SRSC were misidentified and I never did find vouchers for three counties where it was mapped. With regard to these problems, I also checked the counties of distribution given within the Texas Parks and Wildlife Department’s list of rare and endangered species (Poole et al. 2002) against the “Atlas,” as the legal and conservation repercussions could be substantial. Of the approximately 250 listed taxa, 88 had distributions differing from Turner’s maps, and 13 taxa were not even mapped. Whether these 13 taxa were considered synonyms of other taxa or just missed, is unknown.

I disagree with some of his taxonomic conclusions, e.g., in the Euphorbiaceae, which I had been studying, his inclusion of *Chamaesyce simulans*

within *C. theriaca* is not justified. He also recognizes the state and federally listed *Chamaecyfe fendleri* var. *triligulata* as a distinct species, and makes the new combination, but if he would have looked carefully at the Mexican specimens he would see strong intergradation between the two taxa. His synonymizing of var. *wheeleriana* into *Chamaecyfe geyeri* (implied, but not indicated) is also unjustified as they consistently differ in seed and fruit shape.

There are many errors scattered throughout the volumes. There are species listed and mapped under two different names, e.g., *Spiranthes cinnabarina* and *Dichromanthus cinnabarinus* (Orchidaceae); *Festuca pratensis* and *Lolium pratense* (Poaceae); *Salvia dolichantha* and *Salvia whitehouseae* (Lamiaceae). There are many unpublished names in the work, e.g., *Cladium mariscus* var. *jamaicense*, *Scutellaria ovata* var. *texana*, *Teucrium coahuilenum*, and *Croton thermophilus* to name just a few. Interestingly, a synonym for *Salazaria mexicana* is given as *Salvia mexicana* not *Scutellaria mexicana* (Lamiaceae) in a group Turner should know well. In the introduction, Turner transfers some taxa of *Selinocarpus* into *Acleisanthes* (Nyctaginaceae), but in the text, the taxa are given as *Selinocarpus* with the *Acleisanthes* names presented in synonymy, possibly voiding the validity of the new combinations. In the Sapotaceae, *Bumelia* has been placed into *Sideroxylon* and he makes a combination in the introduction changing *S. lanuginosa* subsp. *oblongifolium* to var. *oblongifolium*. But in the text, he uses the name "var. *albicans*," which is not a validly published name in *Sideroxylon*. Also for this taxon, nowhere does he indicate the name *Bumelia* in the synonymy, and as it falls on a page starting with Sapindaceae, nowhere is the family name noted. So for those not familiar with *Sideroxylon*, they are on their own. And then there is the report of *Holosteum umbellatum* (Caryophyllaceae), however the name *Castela stewartii* is noted as a synonym, and when you check the Simaroubaceae you find *Holocantha stewartii* with an almost identical map. So this is another type of error, and whether there actually is a legitimate record *Holosteum* in Texas is unclear. He shows *Ulmus americana* (Ulmaceae) as commonly occurring between Alpine and Marfa, Texas, but those trees are *Ulmus pumila*. There are also many species occurring in Correll and Johnston (1970) that are not in the "Atlas." Some actually may not occur in the flora, others may be considered synonyms, but other well-known taxa are not accounted for in the Atlas' maps. One such interesting plant is the State and Federally Threatened *Helianthus paradoxus*, a much-studied species of hybrid origin between *He-*

lianthus annuus and *H. petiolaris*. Turner (a note in the herbarium) apparently considers these sunflowers to represent a hybrid swarm and he excludes *H. paradoxus* from the "Atlas" even though Welch and Reisberg (2002) give evidence that the taxon, with its Texas and New Mexico populations, appears to be monophyletic and that the original hybridization may have occurred between 75,000 and 208,000 years before present.

But the way I look at it, when it comes to the names used, he has the right use whatever names he wants; it is only his opinion. On the other hand, others need to look carefully at his opinions to determine if they should be followed and not just accept them automatically. The problem, as I see it, is that people may consider his nomenclature authoritative and the final word on the Texas flora.

The "Atlas" would be more user friendly, if for new names, it consistently cited the old names used in the *Manual of the vascular plants of Texas* (Correll and Johnston 1970). This would allow for a direct connection between the two works. The "Atlas" would be even more useful if the pertinent literature involving the name changes was cited. But only a few bibliographic citations are presented with the maps.

Overall, the "Atlas" does what it intended to do, it shows the distribution of native and naturalized plants of Texas, information that has not been brought together in map form previously. And in spite of the problems indicated above, I find the "Atlas" to be very useful and the data very interesting. It is a must-have book for people interested in the flora of Texas.

—JAMES HENRICKSON. Department of Biological Science, California State University, Los Angeles, CA 91030; Visiting Scholar, Plant Resources Center, University of Texas, Austin 78712. henrickson@mail.utexas.edu

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ANNOUNCEMENTS

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APPLICATION NOTICE AND GUIDELINES FOR 2004
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The Annetta Carter Memorial Fund honors Annetta Carter, who devoted the last 40 years of her life to the study of the Baja California flora. Her special interests were floristics, history, biogeography, and ethnobotany of the Sierra de la Giganta.

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Berkeley, CA 94720
smarkos@socrates.berkeley.edu

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2004–2005 SCHEDULE OF SPEAKERS

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University of California, Berkeley

- | | |
|--------------------------|---|
| September 16, 2004 | Raymond Cranfill, University Herbaria, University of California, Berkeley The secret life of ferns |
| October 15, 2004 | James Wanket, Department of Geography, Sacramento State University Relicts and refugia: late Quaternary forests of the Klamath Mountains |
| November 19, 2004 | Susan Lambrecht, Department of Environmental Studies, University of California, Santa Cruz The cost of flowers in ecological currencies |
| January 20, 2005 | James Shevock, National Park Service, Cooperative Ecosystem Studies Unit, University of California, Berkeley Bryogeography of California: what can we learn from the mosses about past and future climate changes? |
| February 19, 2005 | Annual Banquet, Romberg Tiburon Center, Tiburon, CA Arturo Gómez-Pompa, Department of Botany and Plant Sciences, University of California, Riverside Title to be announced |
| March 17, 2005 | Scott Stephens, Department of Environmental Science, Policy and Management, University of California, Berkeley Dynamics of the last, intact, Jeffrey pine ecosystem from northwest Mexico: U.S. restoration implications |
| April 21, 2005 | Elizabeth Wenk, Department of Integrative Biology, University of California, Berkeley Effect of differing substrates on plant physiology and distribution in the alpine Sierra Nevada |
| May 19, 2005 | Michelle McMahon, Department of Evolution and Ecology, University of California, Davis Diversification of floral development in the papilionoid legume tribe Amorpheae |

Seminars are open to all. Refreshments will be served following all seminars.

ERRATUM: CORRECTION TO ODION 2000
POSTFIRE SEEDLING EMERGENCE IN MARITIME CHAPARRAL

DENNIS C. ODION
Institute for Computational Earth Systems Science, University of California,
Santa Barbara, CA 93106

In a previous article (Odion 2000), Table 1 incorrectly reported the numbers of seedlings of four species that emerged following fire at site 2 in the

study. The following are the correct number of seedlings that emerged for each of these four species:

| Species | seedlings/m ² |
|--------------------------------|--------------------------|
| <i>Salvia mellifera</i> | 0.3 |
| <i>Horkelia cuneata</i> | 0.1 |
| <i>Carex globosa</i> | 0.4 |
| <i>Apiastrum angustifolium</i> | 0.3 |

LITERATURE CITED

ODION, DENNIS C. 2000. Seed banks of long-unburned stands of maritime chaparral: Composition, germination behavior and survival with fire. Madroño 47: 195–203.

ERRATUM

Due to an editorial mistake, the authorship of the dedication for volume 50 was not included. The dedication to Wilfred B. Schofield was written by

Judith A. Harpel
c/o Gifford Pinchot National Forest
10600 NE 51st Circle
Vancouver, WA 98682

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MADROÑO

A WEST AMERICAN JOURNAL OF BOTANY

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Editor—DR. JOHN CALLAWAY
Dept. of Environmental Science
University of San Francisco
2130 Fulton Street
San Francisco, CA 94117-1080
callaway@usfca.edu

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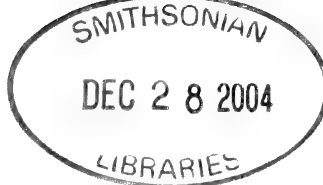
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A VEGETATION MAP OF NAPA COUNTY USING THE MANUAL OF CALIFORNIA VEGETATION CLASSIFICATION AND ITS COMPARISON TO OTHER DIGITAL VEGETATION MAPS

JAMES H. THORNE¹, JEFFERY A. KENNEDY, JAMES F. QUINN, AND MICHAEL MCCOY
Information Center for the Environment, University of California,
Davis, CA 95616

TODD KEELER-WOLF
Wildlife and Habitat Data Analysis Branch, California Department of Fish and
Game, 1807 13th Street, Room 202, Sacramento, CA 95814

JOHN MENKE
Aerial Information Systems, 112 First Street, Redlands, CA 92373

ABSTRACT

In 1995, the *Manual of California Vegetation* introduced a quantitatively based method for classifying and mapping vegetation in California. We used this method to develop a classification of vegetation types for Napa County, which we then used to attribute the polygons of a new vegetation map. The new map was produced by on-screen digitizing over USGS Digital Orthophoto Quarter Quads (DOQQ's) with the aid of ancillary digital maps. We identified the distribution of 56 landcover types, 48 dominated by natural vegetation, at the alliance or aggregated alliance level, in 28,456 polygons across 2042 km². The effective minimum mapping unit is below one hectare. The methods used, the mapping classification system developed, and the extents of landcover types mapped are presented. In a comparison with two previous digital vegetation maps for the area, the US Forest Service's CalVeg and the Gap Analysis Program's GAP maps, the MCV map had finer spatial and floristic resolution. The MCV map has 15 more vegetation types than CalVeg and 22 more vegetation types than GAP. The MCV map contains more riparian corridors and isolated wetlands, identifying 157 km² of these types, compared to 7 km² for CalVeg and a non-spatial result for GAP.

Key Words: vegetation classification, map, GAP, CalVeg, DOQQ, riparian, serpentine.

Physical and biotic conditions, along with site history, drive the composition of plants found at any site (Major 1955; Kent and Coker 1992). Therefore, vegetation represents a unique biotic response to local environmental conditions at a site. Vegetation composition is in turn a major factor in determining what animals may be present. Because of the interactions between environment, plants, vegetation and community structure, vegetation distribution has long interested ecologists and natural resource managers. Documenting regional vegetation is useful for many purposes, including biodiversity assessment, conservation planning, resource management, and species distribution modeling (Stohlgren et al. 1997; Scott and Jennings 1998; Margules and Pressey 2000; Scott et al. 2002; Oliver et al. 2004). At watershed and broader scales, the most common way to document the vegetation is with a spatial map. The basic components of a vegetation map are: a vegetation classification, delineation of the landscape into map units (polygons), and attribution of those map units with classification labels.

This study presents the results of a recently com-

pleted vegetation mapping effort for 2042 km² of Napa County (map available at <http://cain.nbii.gov/regional/napavegmap/>). We developed a vegetation classification at the alliance, the aggregated alliance (Super Alliance) and in a few cases, the finer association level for the county using classification units described in the *Manual of California Vegetation* (MCV) (Sawyer and Keeler-Wolf 1995). Species names follow the Jepson flora (Hickman 1993). We delineated the landscape into map units (polygons) using U.S. Geological Survey (USGS) digital orthophoto quarter quads (DOQQ's), because of their low cost, ready availability, and high spatial resolution. DOQQ's have one-meter pixels and high geospatial accuracy that allowed us to map stands to a target minimum mapping unit (MMU) of one hectare (ha), with a horizontal spatial accuracy that meets USGS map accuracy standards for 1:24000-scale maps (U.S. Geological Survey 1999). Finally, we labeled the polygons using the MCV vegetation classification and an additional list of provisional or aggregated vegetation types, not yet formally defined in the MCV. Methods, results and discussion sections are broken into two parts: the first describes the methodology and the map, while the second compares it to two existing maps. Supplemental map materials not presented in

¹ Author for correspondence, email: jhthorne@ucdavis.edu

this article are available for download at <http://cain.nbii.gov/regional/napavegmap/>.

The techniques presented here are a simple, low cost variant of methods currently being used to map the vegetation of California's National Park units (The Nature Conservancy and Environmental Systems Research Institute 1994a) as well as the California Mojave Desert region (Thomas et al. in press), and other conservation planning areas including western Riverside County.

The *Manual of California Vegetation* (Sawyer and Keeler-Wolf 1995), the principal authority for our map's vegetation types, is the culmination of work coordinated by the California Native Plant Society (CNPS), to develop a consensus classification and standard methodology for floristic descriptions in California. MCV types are based on dominant canopy species that define an alliance and have a correspondingly discernable signature on base map imagery.

The mapped vegetation definitions include size and cover estimates, which permit the conversion (a crosswalk) of MCV-based alliance names to the California Wildlife Habitat Relationship (CWHR) habitat types (Mayer and Laudenslayer 1988; California Department of Fish and Game 2002).

Vegetation Classification System Used

The MCV classification system was selected for the new map for four reasons. First, it is consistent with the National Vegetation Classification Standard (NVCS) hierarchy (The Nature Conservancy and Environmental Systems Research Institute 1994b; Federal Geographic Data Committee 1997) at the alliance and association level. Second, developing the MCV classification through applied mapping projects extends the evolving NVCS floristic classification standard to the montane, mediterranean-climate ecosystems of California. Third, as a quantitatively based classification system, it is objective and repeatable by different investigators, using standard techniques. Finally, it is an adaptive system. As new vegetation types are identified, they may be proposed for inclusion in the MCV. Mapping projects, like this one, play a continuing role in MCV development.

An inter-agency and academic group convened by the CNPS Vegetation Committee developed the MCV vegetation classification (Keeler-Wolf 1993, 1997; Hillyard 1999). It is designed to integrate with the hierarchical NVCS classification. The highest levels are based on dominant growth form, plant physiognomy (e.g., leaf type and seasonality), stand structure, and abiotic factors such as climate, hydrologic regime and geographic region (e.g., "temperate" or "tropical"); while the lowest levels are based on the floristic composition of the vegetation (Grossman et al. 1998). The NVCS has been adopted as a federal agency standard, at the physiognomic level, by the Federal Geographic Data

Committee (FGDC) (1997). The MCV classification is also hierarchical. Finer scale levels of alliance, super-alliance and association may be combined for display at coarser physiognomic levels (formation and class) to show broader vegetation patterns (Grossman et al. 1998; Maybury 1999).

The MCV is an evolving classification system, with new data still being added to the system: over 7500 California vegetation plots of field data have been collected using MCV protocols from 1994 to spring 2003 (Sawyer and Keeler-Wolf 1995; Keeler-Wolf personal observation). The plots have been used to quantitatively describe 415 alliances and over 1450 associations. Ultimately, Keeler-Wolf (personal observation) estimates that some 2000 associations occur in California. For comparison, Maybury (1999) has documented 1642 alliances and 4515 associations nationwide, and NatureServe (<http://www.natureserve.org/>) estimates that there will be 5000–6000 associations nationwide when all fieldwork is completed (Dennis Grossman personal communication, Science Division of NatureServe).

Previous Vegetation Maps

At least five prior maps of the natural vegetation of Napa County exist. Two early maps are the Wieslander Vegetation Type Maps (VTMs) (Wieslander 1935) and Kuchler's 1:1,000,000-scale map (1988). Two more recent digital vegetation maps exist, derived from 30-meter Landsat Thematic Mapper (TM) satellite imagery: the CalVeg map (Schwind and Gordon 2001), and the California Gap Analysis map (GAP) (Thorne 1997; Davis et al. 1998). The CalVeg and GAP maps are compared to the MCV map in this study. A fifth available map, the National Land Cover Database (NLCD), is a national map of physiognomic types, based on Landsat (TM) imagery (Vogelmann et al. 1998).

The CalVeg map was originally used for timber assessment and forest management, but it is now also used for land cover change detection, on a five-year re-mapping cycle. The CalVeg classification emphasizes single species dominance, using an automated supervised classification algorithm, applied to satellite imagery. The greatest species composition detail is provided for tree-dominated (especially conifer) types, with less detail for shrub and herb dominated types. This floristic classification is one of four separate classification components of the CalVeg mapping methodology that identify percent cover, tree size, lifeform and vegetation type (i.e., dominant species). For lifeform, CalVeg identifies 11 types: conifer, hardwoods, mixed conifer and hardwoods, shrub, wet herbaceous, dry herbaceous, barren, water, snow, agricultural and urban. The lifeform category identifies a stand as coniferous if 10% or more of the cover is in conifers. If conifer cover is <10% and hardwood cover is >10%, it is a hardwood type. If there is ≤ 10%

tree cover, but $\geq 10\%$ shrubs cover, it is labeled a shrub polygon. If none of these three categories apply, it is assigned to one of the other categories (Schwind and Gordon 2001).

CalVeg identifies one, two or in rare cases more than two dominant plant species per lifeform polygon. Single species are considered dominant if they occupy $>50\%$ of the dominant lifeform cover. Two species co-dominants are identified under a variety of combinations of cover class, and multiple species are identified for highly diverse types such as enriched mixed conifer forests (Schwind and Gordon 2001). The CalVeg MMU is 1 ha and the map covers most of the forested regions of the state (Schwind and Gordon 2001).

The GAP vegetation map is meant to be used in conjunction with a map representing land management classes to identify, at the ecoregional scale, vegetation types that are poorly represented on lands managed for conservation (Davis et al. 1995). The GAP map identifies up to three dominant overstory plant species in each vegetation type and records up to three vegetation types within each polygon (Holland 1986). Each vegetation class is ranked as to the percentage of the polygon it occupies. GAP converts species combinations into Holland types (Davis et al. 1998), which in turn are converted to CWHR types (Mayer and Laudenslayer 1988). Since publication of the GAP map, CDFG has replaced the Holland classification with the MCV classification and revised CWHR to facilitate a CWHR-MCV crosswalk. The GAP map's MMU is 100 ha, too coarse for most local planning uses. Unlike most other California vegetation maps, GAP covers the entire state and is part of a national program of similar state-level maps.

We used Holland types for comparison to the MCV map, as those are the closest to the vegetation types in the MCV map. To total the spatial distribution of any given Holland type, we multiplied the percentage of that type found in each polygon by that polygon's area and added the results from all the polygons. Note that while total areas can be calculated, the GAP map does not map the locations and extents of Holland types within each polygon.

Study Area

Napa County was selected as the study site because of its floristic, vegetative and environmental diversity, which provided a robust test of the mapping methodology. A biodiversity assessment of Napa County (Underwood and Russell et al. 2001) concluded that existing vegetation maps were of insufficient spatial and floristic resolution to support accurate biodiversity conservation planning. Strong local support for a new vegetation map facilitated the selection of the county, and greatly aided the investigators. Napa County is located north of San Francisco and covers approximately 2042 km².

The flora of Napa County consists of roughly 1520 taxa, based on a draft manuscript of the Flora of Napa County (Jake Ruygt personal communication). Of Napa's 1520 taxa, 1102 are native (present in California pre-settlement, 72.5%) and 418 are exotic (27.5%), compared to 4839 (82.5%) native and 1023 (17.5%) exotic for California's 5862 taxa (Hickman 1993). Thus, Napa County is home to 32% of the state's native flora, while comprising only 0.5% of its total area. This floristic diversity is a function of high climatic, topographic, and edaphic diversity (Ornduff et al. 2004), as well as the overlap of many species at the limit of their ranges (Jake Ruygt personal communication). It leads to a high diversity of vegetation types, many of which are not well documented. This high degree of biodiversity, rarity, and endemism is significant at both statewide and national levels (Stebbins and Major 1978; Stein 2002). The greatest biodiversity occurs in the north county, where elevation and moisture gradients are the steepest and elevations highest (Underwood-Russell et al. 2001).

Physiographically, Napa County exemplifies the California Coast Ranges, with steep, roughly parallel, northwest-trending mountain ridges separated by fertile, flat-bottomed valleys. The county's mediterranean climate has a maritime influence, with a strong, decreasing moisture gradient from west to east and from high to low elevation. Mean annual precipitation ranges from 51 to 140 cm/yr (Daly et al. 1994; Miles and Goudy 1997; Daly et al. 1998). There are 11 broad soil associations (Lambert and Kashiwagi 1978), spread over volcanic, sedimentary and ultramafic (serpentine) terrains (Norris and Webb 1990; Miles and Goudy 1997). The largest watersheds are the Napa and Suisun. The largest lake, Berryessa, is man made and covers 5.7% of the county (determined using the map presented here). Land ownership is predominantly private (Underwood-Russell et al. 2001).

METHODS

Map Development

Map development had five stages: 1) landcover (vegetation) classification and minimum mapping unit (MMU) definition; 2) base map imagery and ancillary GIS data layers acquisition; 3) field reconnaissance to refine the classification and develop a photo interpretation key; 4) vegetation polygon delineation and attribution; and 5) field verification to assess polygon label accuracy and revise polygon definitions and the photo interpretation key, as needed. A five-person crew conducted photo interpretation, polygon delineation and attributing from February to June 2002. A two-person crew conducted field verification from early August through late October 2002.

Landcover classification and target MMU. We developed a list of vegetation types to be mapped by combining a literature review with input from

local botanists. The list contained described vegetation types and vegetation types observed in the county, but for which no formal description (NFD) currently exists. The NFD types were designed to be consistent with the MCV classification hierarchy (Sawyer and Keeler-Wolf 1995). A vegetation type was labeled NFD if: 1) it was not currently in the MCV alliance classification, 2) it was defined in MCV, but could not be distinguished on the imagery from another type, or 3) it was an undefined association within a previously defined MCV alliance. Once a type was identified as NFD, we included it in all subsequent analyses, assuming that it will eventually be described and incorporated in the MCV.

We targeted the vegetation alliance level, rather than the finer association level for polygon labels, because associations are often defined by understory species not visible in remotely sensed imagery, and because associations are less completely defined than alliances for the region (Sawyer and Keeler-Wolf 1995). However, we used the finest hierarchical level discernable on the base imagery, which includes a few associations. Virtually all grasses and many shrub types are not identifiable to species in the imagery, and in forest types, foothill pine (*Pinus sabiniana*) was hard to discern, when its cover was <20%. In these cases, we used the term "super alliance" to indicate an aggregated-alliance, intermediate between a floristic alliance and a physiognomic formation.

Other vegetation data we recorded beyond the vegetation type were: 1) cover classes for all vegetation types, and 2) size classes for tree dominated types only. There are five cover classes, based on percent cover of the dominant stratum: 2–10%, 11–25%, 26–40%, 41–60%, and >60%. There are six size classes: seedlings (<2.5 cm diameter at breast height, DBH), saplings (3–15 cm DBH), small (16–30 cm DBH), medium (31–63 cm DBH), large (>63 cm DBH), and multilayered medium to large trees over smaller trees with combined cover > 60%. Size and cover class for each applicable polygon were recorded to facilitate translation between MCV vegetation and CWHR habitat types (California Department of Fish and Game 2002). A crosswalk between MCV and CWHR classifications allows the MCV map to be used to estimate habitat suitability for vertebrate species and habitat management.

Given the complex, fine grained nature of the vegetation mosaic and the one-meter square size of the 1993 DOQQ imagery, we selected a target MMU of one hectare (2.5 acres), with the caveat that we would delineate smaller polygons, when feasible, for high-value vegetation types such as seeps, riparian corridors, and other wetlands.

Base map imagery and ancillary GIS data. We digitized vegetation polygons and characterized their vegetation from the most recently available

DOQQ's for Napa County, flown in 1993. The following ancillary maps and air photos were used to aid polygon delineation and attributing: 1) 30-meter digital elevation models (DEMs), 2) digital raster graphics (DRGs) of the USGS 1:24,000 topographic maps, 3) the most recent fire history map from the California Department of Forestry and Fire Protection (CDF 1999), 4) the California Division of Land Resource Protection's Farmland Mapping and Monitoring Program (FMMP) maps for Napa County (produced every two years from 1984–1998, we used the 1994 map, <http://www.consrv.ca.gov/DLRP/fmmp/>), 5) color photocopies of ~410 color, 1:24,000 stereo pair aerial photos (WAC Corporation, <http://www.waccorp.com/califcoun.shtml>), 6) color photocopies of the 1931 Wieslander Vegetation Type Maps for southern Napa County, together with the associated VTM plot data and summary descriptive text (from the Dr. Allen-Diaz collection at UC Berkeley), 7) soils and geology maps depicting serpentine terrains (Lambert and Kashiwagi 1978; Wagner et al. 1982), and 8) occurrence maps of vernal pools and selected plant species of concern, provided by Napa County botanist, Jake Rugyt.

Field reconnaissance for classification refinement and photo interpretation key. Field reconnaissance consisted of a three-day, 123-stop driving tour of the county by the project ecologists and photo interpreters that documented vegetation type for 221 vegetation stands. This information was used to: 1) identify previously undocumented vegetation types and revise the vegetation classification scheme; 2) document stands of known composition, structure, and location for use in developing photo interpretation signatures; and 3) collect data on dominant species composition and environmental features at observation points to build vegetation–environment relationship models (developed from Barbour and Major 1988).

Slope, aspect, elevation, substrate, site moisture, land management and disturbance regimes and other environmental factors were recorded at each stop. The initial list of 89 possible vegetation types was distilled into a list of 53 mappable vegetation types, each linked to a vegetation–environment relationship model. Seven non-vegetated or sparsely vegetated land cover types (mudflat, open water, urban, vacant, serpentine barrens, rock outcrop and unidentified), plus agriculture, were also recorded. These observation points allowed the photo interpreters to identify image signatures for known vegetation types. The vegetation–environment relationships and the signature characteristics were then compiled in a photo interpretation key, which was used to attribute unvisited polygons (see <http://cain.nbii.gov/regional/napavegmap/> for the key).

Polygon delineation and labeling. Digitizing was done on-screen, drawing vector outlines of each visible stand of vegetation. In general, the MMU is

1 ha. However, units down to ~ 0.25 ha were delineated around seasonally wet meadows, easily mapped pocket grasslands and farm ponds. Over 5000 polygons are less than 1 ha in size. Polygons were delineated using a larger MMU (~ 2 ha) for subtle divisions between very similar floristic types or to delineate within-type changes in stand size or cover class. A 5-ha MMU was used for urban features within an agricultural polygon or agriculture within urban areas.

Using the photo interpretation key, a team of five photo interpreters digitized and labeled $>31,000$ polygons, each encompassing a stand of vegetation (or non-vegetation cover type) of uniform structure, composition, density and size class (if applicable), as discernable on the DOQQ's. Polygon delineation was recorded on digital 7.5-minute USGS quads, each of which encompasses four 1:12,000-scale DOQQ's. These quads were then merged to create a whole-county map. Ancillary data were used, when appropriate, to facilitate polygon labeling.

Locations of known vegetation were used to start the polygon label attribution process. Photo interpreters trained on these locations, and then identified other, nearby locations of the same vegetation type using the species-environment distribution models and DOQQ image signatures. Vegetation cover and size classes were visually estimated, with the assistance of the ancillary stereo air photo pairs. Size classes were determined using canopy size-diameter at breast height (dbh) regressions available to the air photo interpretation subcontractor (Aerial Information Systems). The total number of polygons was reduced to 28,456 by merging adjacent polygons with identical label attributes.

Field verification and map unit revision. Field verification was done using a preliminary map of the labeled vegetation polygons printed on the imagery at a scale of 1:14000. Field crews drove all available public roads, and as many private roads as we could get permission to access.

When possible, the crews physically entered polygons that were verified. However, most of the field verification consisted of observing nearby slopes with binoculars from viewpoints along road rights-of-way. Verification at a distance was only feasible when the vegetation mosaic allowed extrapolation of the visual signature from nearby, readily identifiable stands to comparable stands over successively larger distances. The majority of the verification distances were <300 m, but for certain forest types with distinctive canopy characteristics, verification was possible at distances up to 600 m.

Field crews documented both correct and incorrectly labeled polygons. For incorrect polygons, an abbreviated Rapid Verification Assessment (RVA) form was used to note the amended vegetation type, attribute features and any new or unusual species. Once a pattern was documented, repeated instances

of the same type of label error were recorded directly on the field maps in abbreviated form. Approximately three team months (two-person teams) were spent checking polygons.

Field verification data were used to make corrections in vegetation type descriptions and for polygon labeling. Field verification data were also collected to refine and correct the species-environment relationship models and the photo interpretation key used to label the polygons. These revisions permitted identification of nearby, unvisited polygons, which might need label corrections. Unvisited polygons requiring attribute edits were assigned a more generalized vegetation type, generally abstracting from alliance level to super-alliance.

Post-production map accuracy assessment. A formal post-production map accuracy assessment was not included in the project due to funding limitations that precluded the field work needed not only for the map accuracy assessment itself, but also for the plot data collection needed to quantitatively define the provisional NFD vegetation types. We chose to use all the verification data to develop the best map we could, given limited resources. We present results from the verification effort.

Map Comparisons

We compared the Napa MCV map to two other available digital vegetation maps: the California Gap Analysis (GAP) map and the US Forest Service CalVeg map. The comparisons are based on: 1) the vegetation classifications used; 2) the extent of different vegetation types mapped; and 3) the number and size distribution of polygons.

Comparison of vegetation classifications. We developed a crosswalk between the three maps' vegetation classification systems by comparing the vegetation classes developed for our mapping effort with the lists of vegetation types from the GAP and CalVeg maps for Napa County. We began by identifying which CalVeg species types and GAP vegetation classes (Holland types) correspond to our MCV types, and which types or classes are unique to one of the three maps. Several GAP or CalVeg classes may correspond to a single MCV class, but we did not allow a single MCV class to go to more than one class in the other systems. Extents of all vegetation classes from all maps are included as part of the mapped extents comparison.

Extent of mapped vegetation types. To compare the extent of mapped vegetation types in the county, we selected an area slightly smaller than the full extent of the county (1835 km^2), since we worked with a version of CalVeg that did not then include a small section of the southern Napa Valley. We clipped the GAP map and the MCV map to the extent of the current CalVeg coverage, then compared the extents of different vegetation types

mapped by each methodology. Vegetation extents were compared for all vegetation types, and condensed into nine groups for more general comparison.

Polygon number and size distribution. We compared the size distribution and number of polygons in each of the three vegetation maps. CalVeg and GAP are regional maps that extend beyond the borders of Napa County, so they were clipped with a county outline. However, clipping the maps created many remnant polygons which had extended outside the county. These internal remnants are often small slivers that do not accurately reflect the true size of those polygons. We used a GIS procedure to exclude the full spatial extent of any polygon that touched the county line, here termed 'internal' for all three maps. This eliminates the problem of comparing partial polygons, reduced in size while clipping. Using the internal form also removed the unmapped section of Napa County from the CalVeg map mentioned above. We also include a version of GAP that includes all polygons that touch the border, named 'external', since there are so few GAP polygons in the county. We then recorded the number of polygons in each map and binned them into 19 size classes, starting with 0.25 (2^{-2}) hectares and doubling in area at each step to a top class of greater than 65,536 (2^{16}) hectares. We removed the Lake Berryessa polygon, the largest single polygon in all maps of the county, before analysis.

RESULTS

The Napa MCV Map

The Napa County MCV map covers 2042.14 km² (Fig. 1; for a copy go to <http://cain.nbii.gov/regional/napavegmap>). We identified 56 landcover types within that area (Table 1). They range widely from common to rare (Table 1, Fig. 2). Four types are human related or non-vegetative: Urban or Built up, Agriculture, Vacant, and Water. An additional three types are defined by geology or geomorphic processes rather than by vegetation: Rock Outcrop, Serpentine Barrens, and Riverine, Lacustrine and Tidal Mudflats. These rock types likely have sparse annual plants that cannot be mapped to the alliance level using DOQQ's or remotely sensed imagery.

Of the 48 vegetation-dominated cover types, 28 were previously defined MCV types, at the following hierarchical levels: three formations, one super alliance, 23 alliances and one restoration type. The remaining 20 vegetation types were not formally defined (NFD): ten NFD super alliances, two NFD alliances and eight NFD associations.

The three most extensive vegetation types are: Blue Oak (*Quercus douglasii*) alliance, California Annual Grasslands alliance, and Chamise (*Adenostoma fasciculatum*) Chaparral alliance. The three types with the least mapped extent are the California Juniper (*Juniperus californica*) alliance, Sugar Pine—Canyon Live Oak (*Pinus lambertiana*—*Quercus chrysolepis*) super alliance, and the Coyote Bush—California Sagebrush—Lupine spp. (*Baccharis pilularis*—*Artemisia californica*—*Lupinus* spp.) super alliance. Three vegetation types largely represent non-native plants: Eucalyptus alliance, Upland Annual Grasslands and Forbs and California Annual Grasslands. Forty-five types are dominated by native vegetation.

Agriculture occupies 12.5% of the county, water and urban total 5.7% and 5.2%, respectively. In aggregate, the five cover types that represent the human-mediated removal of natural vegetation cover encompass 24.1% of the county, exclusive of San Pablo Bay, leaving 75.9% with natural or semi-natural vegetative cover. Fifty percent of the vegetation types occupy in aggregate five percent of the land (Table 1). Note that water is almost exclusively a human-dominated cover type, because all mapped bodies of open water are either artificial reservoirs, agricultural irrigation ponds, or inundated, diked bay flats.

Vegetation classification and field verification. During field verification, 3108 polygons were observed, representing ~11% of total polygons. Of the 3108, 1001 (32.5%) required some degree of correction, 200 polygons (6.2%) initially labeled 'unknown' were assigned to a cover type (not considered an error), and 1907 were judged to be entirely correct (61.3%). In most cases, editing changes were minor (e.g., correcting one of two oak species in a mixed oak alliance). An additional 1243 polygons flagged as 'unknown' types by the photo interpreters, were not field visited, due to limited access. The changes recorded in polygon labels were then applied in a GIS environment to make changes to nearby, similar, but unvisited polygon labels. Finally, a small number of polygons (203, totaling 0.3% of the county's area, 0.7% of all polygons) were unidentifiable on the base imagery and remain unclassified.

Analysis of the field verification data resulted in a reduction of the initial, pre-reconnaissance natural and semi-natural vegetation classification from 53 to 48 types.

This reduction reflected the inability of the photo interpreters to reliably distinguish foothill pine in

FIG. 1. Vegetation map of Napa County using the Manual of California Vegetation Classification. This map represents the results of the MCV mapping effort in Napa County and depicts 56 land cover types in 28,456 polygons across 2,042 km². The legend lists the cover types in the same order as in Table 1. Landcover types found on serpentine are indicated in hues of purple and pink.

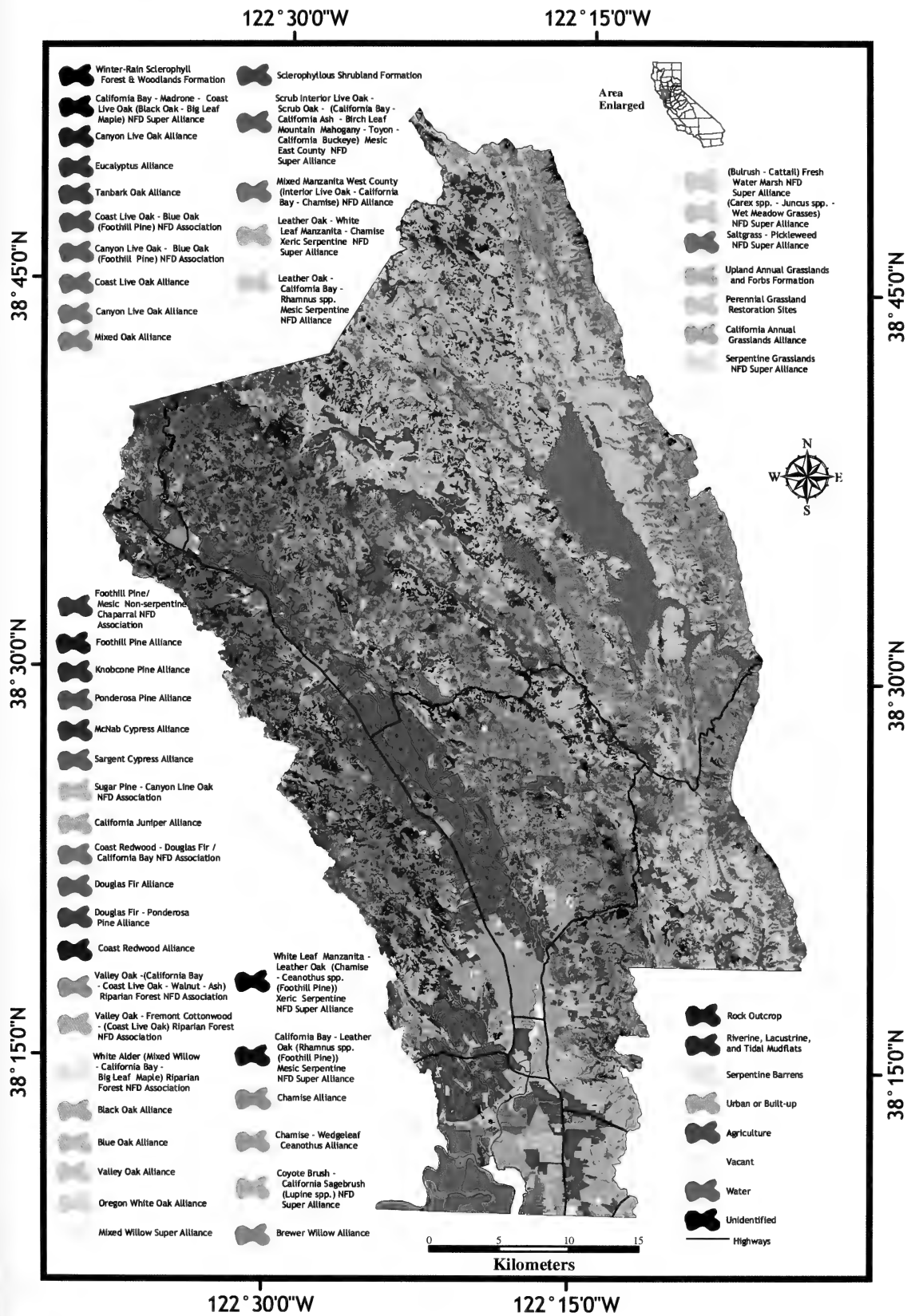


TABLE 1. SPATIAL EXTENT OF MANUAL OF CALIFORNIA VEGETATION TYPES IN NAPA COUNTY. Area measurements for each landcover type are shown. The table shows the percent of the county occupied by each landcover type; the rank order by area in descending order; and the number of polygons in each type. The code represents the numbers assigned in the GIS version of the map and is included for reference along with species names according to the Jepson Flora (Hickman 1993).

| Code | Cover type | Area (ha) | % Total area | Area rank order | Number of polygons |
|------|---|-----------|--------------|-----------------|--------------------|
| 1100 | Winter-Rain Sclerophyll Forests and Woodlands Formation | 250.6 | 0.1 | 40 | 60 |
| 1101 | California Bay-Madrone-Coast Live Oak-(Black Oak-Big Leaf Maple) NFD Super Alliance (<i>Umbellularia californica</i> - <i>Arbutus menziesii</i> - <i>Quercus agrifolia</i> (<i>Quercus kelloggii</i> - <i>Acer macrophyllum</i>)) | 7423.6 | 3.6 | 10 | 849 |
| 1122 | Canyon Live Oak Alliance (<i>Quercus chrysolepis</i>) | 229.2 | 0.1 | 41 | 22 |
| 1123 | Eucalyptus Alliance (<i>Eucalyptus</i> spp.) | 165 | 0.08 | 46 | 52 |
| 1124 | Tanbark Oak Alliance (<i>Lithocarpus densiflorus</i>) | 99.3 | 0.05 | 51 | 9 |
| 1201 | Coast Live Oak-Blue Oak-(Foothill Pine) NFD Association (<i>Quercus agrifolia</i> - <i>Quercus douglasii</i> (<i>Pinus sabiniana</i>)) | 10,734.8 | 5.26 | 8 | 1840 |
| 1202 | Canyon Live Oak-Blue Oak-(Foothill Pine) NFD Association (<i>Quercus chrysolepis</i> - <i>Quercus douglasii</i> (<i>Pinus sabiniana</i>)) | 7315.5 | 3.58 | 11 | 1243 |
| 1221 | Coast Live Oak Alliance (<i>Quercus agrifolia</i>) | 5332.9 | 2.6 | 13 | 1597 |
| 1222 | Interior Live Oak Alliance (<i>Quercus wislizenii</i>) | 2161.7 | 1.06 | 23 | 374 |
| 1223 | Mixed Oak Alliance (<i>Quercus</i> spp.) | 11,659.4 | 5.7 | 5 | 1814 |
| 2104 | Foothill Pine/Mesic non-serpentine chaparral NFD Association (<i>Pinus sabiniana</i>) | 382.1 | 0.2 | 39 | 84 |
| 2121 | Foothill Pine Alliance (<i>Pinus sabiniana</i>) | 717.2 | 0.35 | 34 | 144 |
| 2122 | Knobcone Pine Alliance (<i>Pinus attenuate</i>) | 2401.1 | 1.18 | 21 | 374 |
| 2123 | Ponderosa Pine Alliance (<i>Pinus ponderosa</i>) | 68.1 | 0.03 | 52 | 5 |
| 2124 | McNab Cypress Alliance (<i>Cupressus macnabiana</i>) | 981 | 0.5 | 29 | 131 |
| 2125 | Sargent Cypress Alliance (<i>Cupressus sargentii</i>) | 742.8 | 0.36 | 32 | 31 |
| 2126 | Sugar Pine-Canyon Oak NFD Association (<i>Pinus lambertiana</i> - <i>Quercus chrysolepis</i>) | 1.4 | 0.001 | 55 | 1 |
| 2127 | California Juniper Alliance (<i>Juniperus californica</i>) | 1 | 0.00 | 56 | 1 |
| 2201 | Coast Redwood-Douglas Fir/California Bay NFD Association (<i>Sequoia sempervierens</i> - <i>Pseudotsuga menziesii</i> (<i>Umbellularia californica</i>)) | 1164.7 | 0.57 | 28 | 92 |
| 2222 | Douglas Fir Alliance (<i>Pseudotsuga menziesii</i>) | 7032.5 | 3.44 | 12 | 781 |
| 2224 | Douglas Fir-Ponderosa Pine Alliance (<i>Pseudotsuga menziesii</i> - <i>Pinus ponderosa</i>) | 3794.4 | 1.9 | 16 | 305 |
| 2230 | Coast Redwood Alliance (<i>Sequoia sempervierens</i>) | 131 | 0.06 | 47 | 8 |
| 3101 | Valley Oak-(California Bay-Coast Live Oak-Walnut-Ash) Riparian Forest NFD Association (<i>Quercus lobata</i> -(<i>Umbellularia californica</i> - <i>Quercus agrifolia</i> - <i>Juglans californica</i> - <i>Fraxinus dipetala</i>)) | 2313.6 | 1.13 | 22 | 206 |
| 3102 | Valley Oak-Fremont Cottonwood (Coast Live Oak) Riparian Forest NFD Association (<i>Quercus lobata</i> - <i>Populus fremontii</i> (<i>Quercus agrifolia</i>)) | 210.3 | 0.1 | 43 | 31 |
| 3121 | Black Oak Alliance (<i>Quercus kelloggii</i>) | 898.4 | 0.4 | 30 | 91 |
| 3122 | Blue Oak Alliance (<i>Quercus douglasii</i>) | 17,883.8 | 8.76 | 2 | 2992 |
| 3123 | Valley Oak Alliance (<i>Quercus lobata</i>) | 1310 | 0.64 | 27 | 333 |
| 3124 | Oregon White Oak Alliance (<i>Quercus garryana</i>) | 459.4 | 0.23 | 37 | 83 |
| 3201 | White Alder (Mixed Willow-California Bay-Big Leaf Maple) Riparian Forest NFD Association (<i>Alnus rhombifolia</i> (<i>Salix</i> spp.)- <i>Umbellularia californica</i> - <i>Acer macrophyllum</i>) | 391.1 | 0.19 | 38 | 46 |
| 3202 | Brewer Willow Alliance (<i>Salix breweri</i>) | 112.2 | 0.06 | 48 | 29 |
| 3221 | Mixed Willow Super Alliance (<i>Salix</i> spp.) | 218.3 | 0.1 | 42 | 85 |
| 4300 | Sclerophyllous Shrubland Formation | 1325.4 | 0.7 | 26 | 283 |
| 4301 | Scrub Interior Live Oak-Scrub Oak-(California Bay-California Ash-Birch Leaf Mountain Mahogany-Toyon-California Buckeye) Mesic East Count NFD Super Alliance (<i>Quercus wislizenii</i> var. <i>frutenscens</i> - <i>Quercus berberidifolia</i> -(<i>Umbellularia californica</i> - <i>Fraxinus dipetala</i> - <i>Cercocarpus betuloides</i> - <i>Heteromeles arbutifolia</i> - <i>Aesculus californica</i>)) | 4471.9 | 2.2 | 15 | 985 |

TABLE 1. CONTINUED.

| Code | Cover type | Area (ha) | % Total area | Area rank order | Number of polygons |
|------|--|-----------|--------------|-----------------|--------------------|
| 4302 | Mixed Manzanita–(Interior Live Oak–California Bay–Chamise) West County NFD Alliance (<i>Quercus wislizenii</i> – <i>Umbellularia californica</i> – <i>Adenostoma fasciculatum</i>) | 3570.7 | 1.8 | 17 | 810 |
| 4303 | Leather Oak–White Leaf Manzanita–Chamise Xeric Serpentine NFD Super Alliance (<i>Quercus durata</i> – <i>Arctostaphylos viscida</i> – <i>Adenostoma</i>) | 10,915.2 | 5.4 | 7 | 1352 |
| 4304 | Leather Oak–California Bay–Rhamnus spp. Mesic Serpentine NFD Super Alliance (<i>Quercus durata</i> – <i>Umbellularia californica</i>) | 1797 | 0.9 | 24 | 397 |
| 4305 | Whiteleaf Manzanita–Leather Oak–(Chamise–Ceanothus spp. (Foothill Pine)) Xeric Serpentine NFD Super Alliance (<i>Arctostaphylos viscida</i> – <i>Quercus durata</i> (<i>Adenostoma</i> – <i>ceanothus</i> (<i>Pinus sabiniana</i>))) | 3225 | 1.6 | 18 | 624 |
| 4306 | California Bay–Leather Oak–(Rhamnus spp. (Foothill Pine)) Mesic Serpentine NFD Super Alliance (<i>Umbellularia californica</i> – <i>Quercus durata</i> (<i>Pinus sabiniana</i>))) | 2951.5 | 1.5 | 19 | 463 |
| 4321 | Chamise Alliance (<i>Adenostoma fasciculatum</i>) | 12,443.4 | 6.1 | 4 | 2656 |
| 4322 | Chamise–Wedgeleaf Ceanothus Alliance (<i>Adenostoma fasciculatum</i> – <i>Ceanothus cuneatus</i>) | 2814 | 1.4 | 20 | 439 |
| 4501 | Coyote Brush–California Sagebrush (Lupine spp.) NFD–Super Alliance (<i>Baccharis pilularis</i> – <i>Artemisia californica</i>) | 17.1 | 0.008 | 54 | 8 |
| 6402 | (Bulrush–Cattail) Fresh Water Marsh NFD Super Alliance (<i>Scirpus</i> spp– <i>Typha</i> spp) | 109.7 | 0.05 | 49 | 50 |
| 6403 | (<i>Carex</i> spp.– <i>Juncus</i> spp.–Wet Meadow Grasses) NFD Super Alliance | 168.4 | 0.08 | 45 | 82 |
| 6501 | Saltgrass–Pickleweed NFD Super Alliance (<i>Distichlis</i> sp– <i>Salicornia</i> sp) | 1444.6 | 0.71 | 25 | 45 |
| 7100 | Upland Annual Grasslands and Forbs Formation | 4921.7 | 2.4 | 14 | 408 |
| 7101 | Native Grassland Restoration Sites | 103.6 | 0.05 | 50 | 3 |
| 7120 | California Annual Grasslands Alliance | 15,903 | 7.8 | 3 | 2528 |
| 7130 | Serpentine Grassland NFD–Super Alliance | 843.9 | 0.4 | 31 | 591 |
| 9001 | Rock Outcrop | 703.4 | 0.34 | 35 | 331 |
| 9002 | Riverine, Lacustrine and Tidal Mudflats | 174.5 | 0.09 | 44 | 22 |
| 9003 | Serpentine Barrens | 18 | 0.009 | 53 | 17 |
| 9100 | Urban or Built-up | 10,702.6 | 5.24 | 9 | 716 |
| 9200 | Agriculture | 25,991.5 | 12.8 | 1 | 769 |
| 9300 | Vacant | 722.8 | 0.4 | 33 | 193 |
| 9400 | Water | 11,653.5 | 5.7 | 6 | 768 |
| 9999 | Unidentified | 635.3 | 0.3 | 36 | 203 |
| | Total: | 204,213.5 | 100 | | 28,456 |

several of the preliminary vegetation classes where that species was frequently observed to be a sparse dominant in the upper tree canopy. As a consequence, these vegetation types were redefined on the basis of their remaining co-dominants, and Foothill Pine was listed as a parenthetical species or was eliminated from the name, but mentioned in the cover type description (see <http://cain.nbii.gov/regional/napavegmap> for a description of all Napa MCV vegetation types). The Serpentine Barrens category was added, because it is habitat for a variety of rare or endemic annual species and was used to re-label all Rock Outcrops that overlap serpentine on the geology or soils maps.

Map Comparisons

Number and size of polygons. The number of polygons in the MCV map totaled 28,456, compared to 28,918 for CalVeg and 69 for GAP. For the internal versions, there were 27,456 MCV polygons, versus 27,435 for CalVeg and 29 for GAP. Mean and median (internal) polygon sizes are within one hectare for the MCV and CalVeg maps, while the GAP polygon mean and median are three orders of magnitude larger. The MCV map has the smallest standard deviation in polygon size, followed by CalVeg and GAP (Table 2).

MCV has 5415 polygons (19.7% of all MCV

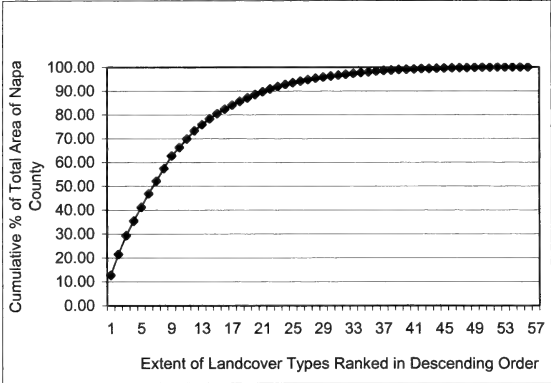


FIG. 2. Area cumulative percent chart. This chart shows the increasing area of Napa County covered as landcover types are added to the map in rank order.

polygons) that are smaller than the smallest polygon in either the CalVeg (1 ha) or the GAP (100 ha) maps (Table 2). While the MCV has polygons smaller than CalVeg, the numbers of polygons in the larger size classes of the two maps are comparable. GAP polygons are much larger; the smallest GAP polygon is larger than 99.1% of the MCV polygons and 99.5% of the CalVeg polygons.

The shape and spatial configuration of polygons differ for each map (Fig. 3a, b, c). CalVeg polygons

have a stair-stepped edge appearance, resulting from the 30 m pixels of the Landsat TM base map imagery. MCV and GAP maps have smooth curvilinear outlines but are at very different scales. We did not attempt to quantify edge differences.

Classification crosswalks and vegetation type extents. For clarity, we only allowed each MCV vegetation type to correspond to a single CalVeg or GAP type. However, we allowed CalVeg and GAP types to link to one or more MCV types. The comparisons listed here were done on the 1835 km² sub-region of the county, the area covered by the CalVeg map (~90% of the county).

The Napa GAP map has 36 cover types, 10 of which cover human land use types, open water, barren land and eucalyptus, leaving 26 vegetative types. The CalVeg map has 46 cover types, nine of which cover human land use types, eucalyptus, open water and barren sites. We compared all possible types, focusing on the 48 MCV, 26 GAP, and 37 CalVeg natural vegetation types (Table 3).

Only the MCV map identifies 'Rock Outcrops' as a cover type. The closest type for CalVeg and GAP is 'Barren'. 'Rock outcrop' contains some vegetative potential, as many plant species grow sparsely in rocky areas. The same applies for the MCV 'Serpentine Barrens' type, which had no direct match in the other classification systems. MCV has a term for a potential aquatic plant habitat,

TABLE 2. POLYGON SIZE DISTRIBUTION COMPARISON FOR THREE DIGITAL VEGETATION MAPS OF NAPA COUNTY. Polygons touching the border of Napa county, and Lake Berryessa have been excluded in the 'internal' versions. Border polygons are completely included in the GAP 'external' column.

| Polygon size distribution by hectare size class | Number of MCV polygons, internal | Number of CalVeg polygons, internal | Number of GAP polygons, internal | Number of GAP polygons, external |
|---|----------------------------------|-------------------------------------|----------------------------------|----------------------------------|
| 0-0.25 | 327 | 0 | 0 | 0 |
| 0.5 | 1237 | 0 | 0 | 0 |
| 1 | 3851 | 0 | 0 | 0 |
| 2 | 6244 | 8927 | 0 | 0 |
| 4 | 6412 | 10,113 | 0 | 0 |
| 8 | 4798 | 5452 | 0 | 0 |
| 16 | 2685 | 1890 | 0 | 0 |
| 32 | 1199 | 623 | 0 | 0 |
| 64 | 449 | 258 | 0 | 0 |
| 128 | 144 | 91 | 1 | 2 |
| 256 | 67 | 30 | 3 | 3 |
| 512 | 30 | 17 | 1 | 2 |
| 1024 | 4 | 7 | 3 | 7 |
| 2048 | 8 | 4 | 7 | 11 |
| 4096 | 0 | 1 | 8 | 15 |
| 8192 | 0 | 0 | 5 | 14 |
| 16,384 | 0 | 1 | 0 | 11 |
| 32,768 | 0 | 0 | 1 | 2 |
| 65,536 | 0 | 0 | 0 | 1 |
| Total # polygons | 27,455 | 27,434 | 28 | 68 |
| Average size polygon (ha) | 6.7 | 5.8 | 3072.3 | 5290.4 |
| Median size polygon (ha) | 2.5 | 2.7 | 1923.7 | 3063.5 |
| Standard deviation (ha) | 33.4 | 59.1 | 3953.2 | 6079.0 |
| Polygon size range hectares (ha) | 0.001-1964.0 | 1.01-8307.5 | 120.8-20,390.2 | 110.8-33,680.8 |

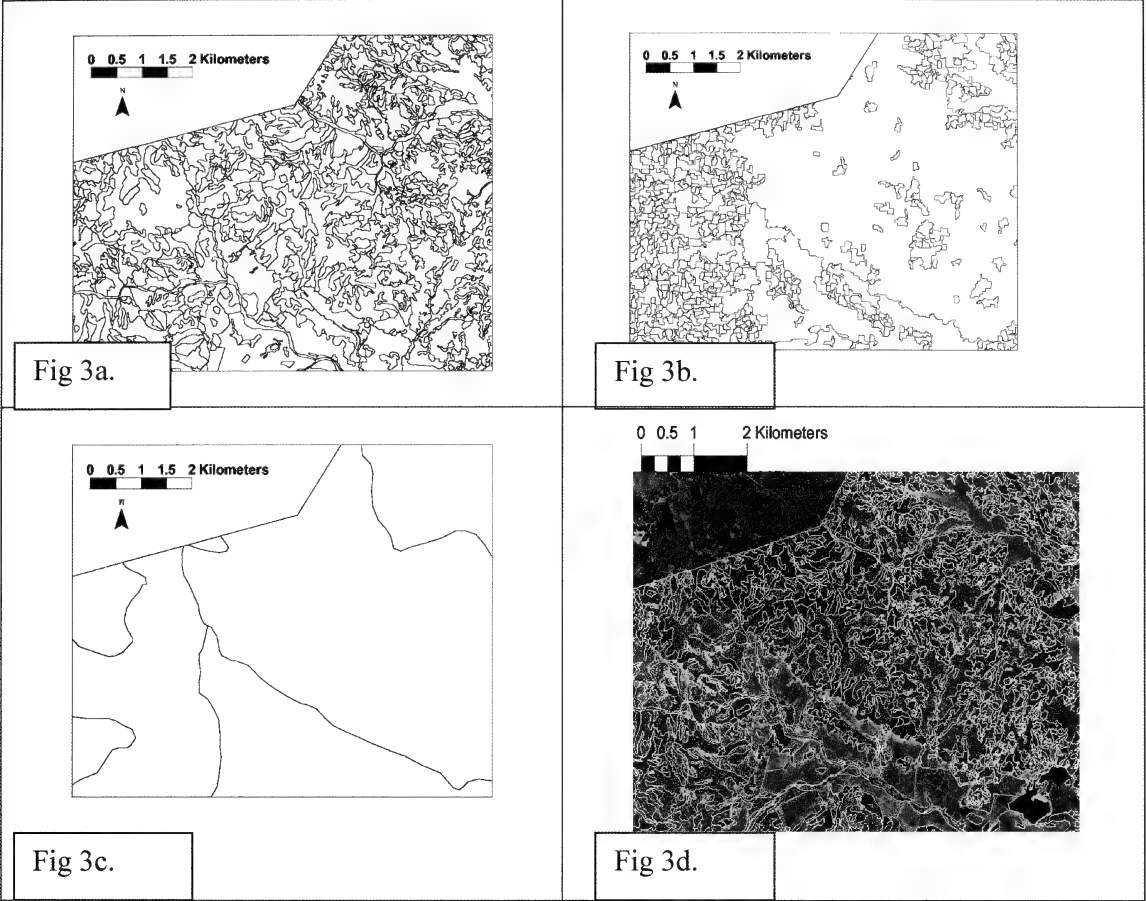


FIG. 3. Polygon shape differences. Figures 3a–c illustrate the differences in polygons between a section of the three maps compared in this study. Figure 3a shows the MCV map, 3b the CalVeg map, and 3c the GAP map. Figure 3d shows the MCV map underlain by the Digital Ortho Photo Quad imagery used as the basis for polygon delineation.

‘Riverine, Lacustrine and Tidal Mudflats’. GAP has two similar terms, ‘Bays and Estuaries’ and ‘Streams and Canals’. MCV has six specifically named serpentine types, CalVeg has one and GAP two.

MCV compared to GAP. Of the 26 vegetation types in GAP, ten correspond to a single MCV type. Two MCV types, Douglas-fir (*Pseudotsuga menziesii*) alliance (2222) and Foothill Pine (*Pinus sabiniana*) alliance (2121) have three GAP types associated with them. Six MCV types have two GAP types in them (Table 3). GAP has a method of identifying cover density in the class name, with some hardwoods listed separately as both woodland and forest. This naming convention accounts for three of the doubled crosswalk links, which would go to individual MCV types if we used the MCV cover attribute (not presented here). The GAP map does not explicitly map riparian vegetation types because they generally fall below GAP’s target MMU of 100 ha. However, GAP lists 921 ha of Valley Oaks (*Quercus lobata*), which may include a riparian

phase (Table 3), and 21 of the 69 GAP polygons list riparian species as present.

MCV compared to CalVeg. Of the 37 CalVeg types, 23 correspond to a single MCV type. CalVeg maps one type, California Buckeye (*Aesculus californica*) (QI, 15.8 ha), that is not currently in the Napa MCV map. Buckeye is a listed alliance in the MCV (Sawyer and Keeler-Wolf 1995), but its typically small stands were not mapped.

Seven CalVeg types describe 19 MCV types: two CalVeg types, Productive Hardwoods (NX) and Foothill Pine (PD), correspond to four MCV types each; one CalVeg type, Barren (BA), corresponds to three MCV types; and, four CalVeg types, Valley Oak (QL), Willow (QO), Lower Montane Mixed Chaparral (CQ), and Ultramafic Mixed Shrub (C1) correspond to two MCV types each. Three MCV types have two CalVeg types associated with them: Coyote Bush (4501), California Bay—Madrone—Coast Live Oak (Black Oak—Big Leaf Maple) (*Umbellularia californica*—*Arbutus menziesii*—*Quercus agrifolia* (*Quercus kelloggii*—*Acer macro-*

TABLE 3. VEGETATION CLASS EXTENTS FROM THE MCV, CALVEG AND GAP VEGETATION MAPS OF NAPA COUNTY. MCV vegetation classes listed, with corresponding CalVeg and GAP vegetation classes on the same row and subsequent rows. CalVeg and GAP types that apply to more than one MCV class are listed at each MCV class they correspond to, the second and subsequent times in hard brackets [: the spatial extents are listed only after the first record. Categories not comparable with MCV types are listed at the bottom of each subsection. CalVeg and GAP types that correspond to MCV types but were not mapped in Napa are included for cross-reference purposes, receiving zeros for their area extents.

| MCV vegetation type classes | CalVeg alliance type | GAP/CNDDDB type classes | MCV mapped hectares | CalVeg mapped hectares | GAP mapped hectares | MCV type codes | CalVeg type codes | GAP CNDDDB codes |
|---|-------------------------------|--|---------------------|------------------------|---------------------|----------------|-------------------|------------------|
| Hardwood Types | | | | | | | | |
| Winter-Rain Sclerophyll Forests and Woodlands Formation | | | 235.3 | | | 1100 | | |
| California Bay–Madrone–Coast Live Oak–(Black Oak–Big Leaf Maple) NFD Super Alliance | California Bay | | 7317.8 | 18.9 | | 1101 | QB | |
| Coast Live Oak Alliance | Mixed Hardwood Coast Live Oak | Coast Live Oak Forest | 4939.9 | 32,310.0 1845.3 | 14,588.5 1972 | 1221 | NX QA | 81310 71160 |
| Coast Live Oak–Blue Oak–(Foothill Pine) NFD Association | [Mixed Hardwoods] | Coast Live Oak Woodland | 10,664.2 | | | 1201 | [NX] | |
| Interior Live Oak Alliance | Interior Live Oak | Interior Live Oak Forest | 2150.8 | 2006.1 | 4715.7 1207.6 | 1222 | QW | 81330 71150 |
| Interior Live Oak–Blue Oak–(Foothill Pine) NFD Association | [Mixed Hardwoods] | Interior Live Oak Woodland | 7371.3 | | | 1202 | [NX] | |
| Black Oak Alliance | Black Oak | Black Oak Forest | 885.1 | 434.3 | 1530.4 | 3121 | QK | 81340 71120 |
| Blue Oak Alliance | Blue Oak | Blue Oak Woodland | 17,965.0 | 22,645.6 | 19,539.2 | 3122 | QD | 71140 |
| Oregon White Oak Alliance | Oregon White Oak | Oregon Oak Woodland | 447.1 | 528.1 | 2913 | 3124 | QG | 71110 71420 |
| | | Mixed North Slope Cis-montane Woodland (in part) | | | 10,300.5 | | | |
| Valley Oak Alliance | Valley Oak | Valley Oak Woodland | 1023.0 | 452.9 | 920.5 | 3123 | QL | 71130 |
| Tanbark Oak Alliance | Tanoak (Madrone) | | 101.6 | 4.7 | | 1124 | QT | |
| Canyon Live Oak Alliance | Canyon Live Oak | Canyon Live Oak Forest | 225.9 | 329.3 | 1870.6 | 1122 | QC | 81320 |
| Mixed Oak Alliance | Productive Mixed Hardwoods | | 11,424.4 | 1795.0 | | 1223 | TX | |
| | [Mixed Hardwoods] | | | | | | [NX] | |
| | California Buckeye | | | 15.8 | | | QI | |
| Coniferous Types | | | | | | | | |
| Foot Pine Alliance | Gray Pine | Open Foot hill Pine Woodland | 710.2 | 5877.3 | 1864.3 | 2121 | PD | 71310 |
| | | Foothill Pine-Oak Woodland | | | 29,689 | | | 71410 |
| Foothill Pine/Mesic non-serpentine chaparral NFD Association | [Gray Pine] | Non-Serpentine Foothill Pine Woodland | 373.8 | | 9302.7 | 2104 | [PD] | 71322 |

TABLE 3. CONTINUED.

| MCV vegetation type classes | CalVeg alliance type | GAP/CNDDDB type classes | MCV mapped hectares | CalVeg mapped hectares | GAP mapped hectares | MCV type codes | CalVeg type codes | GAP CNDDDB codes |
|--|--|--|---------------------------|------------------------------|---------------------------|----------------------|-------------------------|------------------------|
| Douglas Fir Alliance | Pacific Douglas Fir | Upland Douglas Fir Forest Mixed Evergreen Forest (in part) | 7090.6 | 5474.2 | 1251.2 3984 | 2222 | DF | 82420 81100 |
| | | Coast Range Mixed coniferous Forest | | | 8013.6 | | | 84110 |
| Douglas Fir–Ponderosa Pine Alliance | Douglas Fir/Pine Mixed Conifer–Pine | | 3819.2 | 2931.0 | | 2224 | DP | |
| Ponderosa Pine Alliance | Ponderosa Pine | | 68.9 | 107.3 | | 2123 | MP | |
| California Juniper Alliance | | | 1.0 | 491.6 | | 2127 | PP | |
| Coast Redwood Alliance | Redwood | | 124.7 | 0.0 | | 2230 | RW | |
| Coast Redwood–Douglas Fir/California Bay NFD Association | Redwood–Douglas Fir | | 1178.8 | 1334.9 | | 2201 | RD | |
| Knobcone Pine Alliance | Knobcone Pine | Knobcone Pine Forest | 2382.1 | 1015.5 | 3244.5 | 2122 | KP | 83210 |
| McNab Cypress Alliance | McNab Cypress | | 978.1 | 1566.1 | | 2124 | MN | |
| Sargent Cypress Alliance | Sargent Cypress | | 820.6 | 781.0 | | 2125 | MS | |
| Sugar Pine–Canyon Oak NFD Association | | | 1.3 | | | 2126 | | |
| Riparian Types | | | | | | | | |
| Valley Oak–(California Bay–Coast Live Oak–Walnut–Ash) Riparian Forest NFD Association | [Valley Oak] | | 1670.2 | | | 3101 | [QL] | |
| Valley Oak–Fremont Cottonwood (Coast Live Oak) Riparian Forest NFD Association | Fremont Cottonwood | | 64.9 | 0.0 | | 3102 | QF | |
| White Alder (Mixed Willow–California Bay–Big Leaf Maple) Riparian Forest NFD Association | Mixed Riparian Hardwood | | 234 | 337.6 | | 3201 | NR | |
| Mixed Willow Super Alliance | Willow [Willow] | | 119.2 | 19.3 | | 3221 | QO | |
| Brewer Willow Alliance | | | 60.3 | | | 5222 | [QO] | |
| Hard Chaparral Types | | | | | | | | |
| Sclerophyllous Shrubland Formation | Lower Montane Mixed Chaparral | Buck Brush Chaparral | 1323.3 | 37,695.0 | 4807.8 | 4300 | CQ | 37810 |
| Scrub Interior Live Oak–Scrub Oak–(Cal. Bay–Cal. Ash–Birch Leaf Mountain Mahogany–Toyon–Cal. Buckeye) Mesic East County NFD Super Alliance | Scrub Oak | | 4303.6 | 2479.1 | | 4301 | CS | |
| Mixed Manzanita–(Interior Live Oak–California Bay–Chamise) West County NFD Alliance | [Lower Montane Mixed Chaparral] | Northern Mixed Chaparral | 3470.1 | | 8156* | 4302 | [CQ] | |

TABLE 3. CONTINUED.

| MCV vegetation type classes | CalVeg alliance type | GAP/CNDDDB type classes | MCV mapped hectares | CalVeg mapped hectares | GAP mapped hectares | MCV type codes | CalVeg type codes | GAP CNDDDB codes |
|--|-----------------------------------|---|---------------------------|------------------------------|---------------------------|----------------------|-------------------------|------------------------|
| Leather Oak–White Leaf Manzanita–Chamise Xeric Serpentine NFD Super Alliance | Ultramafic Mixed Shrub Alliance | | 11,035.4 | 0.0 | | 4303 | C1 | |
| Leather Oak–California Bay–Rhamnus spp. Mesic serpentine NFD Super Alliance | [Ultramafic Mixed Shrub Alliance] | | 1766.9 | | | 4304 | [C1] | |
| Whiteleaf Manzanita–Leather Oak–(Chamise–Ceanothus spp. (Foothill Pine)) Xeric Serpentine NFD Super Alliance | [Gray Pine] | Serpentine Foothill Pine–Chaparral Woodland | 3221.7 | | 2177.5 | 4305 | [PD] | 71321 |
| California Bay–Leather Oak–(Rhamnus spp. (Foothill Pine)) Mesic Serpentine NFD Super Alliance | [Gray Pine] | | 2905.5 | | | 4306 | [PD] | |
| Chamise Alliance | Chamise Ceanothus Chaparral | Chamise Chaparral | 12,390.0 | 6723.8 | 3798.4 | 4321 | CA | 37200 |
| Chamise–Wedgeleaf Ceanothus Alliance | Wedgeleaf Ceanothus | Mixed Serpentine Chaparral | 2820.0 | 50.4 | 297.7 | 4322 | CC | 37610 |
| | | | | 15.1 | | | CL | |
| Soft Chaparral Types | | | | | | | | |
| Coyote Brush–California Sagebrush (Lupine spp.) NFD Super Alliance | Coyote Bush | | 12.2 | 8.6 | | 4501 | CK | |
| | Mixed Soft Scrub Chaparral | | | 20.4 | | | SQ | |
| Grassland Types | | | | | | | | |
| Upland Annual Grasslands and Forbs Formation | Annual Grass–Forb | | 3001.0 | 22,749.4 | | 7100 | HG | |
| Native Grassland Restoration Sites | [Annual Grass–Forb] | | 105.2 | | | 7101 | [HG] | |
| California Annual Grasslands Alliance | [Annual Grass–Forb] | Non-Native Grassland | 15,175.8 | | 10,314.4* | 7120 | [HG] | 42200 |
| | | Coastal Prairie | | | 2819.3 | | | 41000 |
| Serpentine Grassland NFD Super Alliance | [Annual Grass–Forb] | | 732.7 | | | 7130 | [HG] | |
| Wetland Types | | | | | | | | |
| (Bulrush–Cattail) Fresh Water Marsh NFD Super Alliance | Tule–Cattail | | 71.6 | 0.0 | | 6402 | HT | |
| (Carex spp.–Juncus spp.–Wet Meadow Grasses) NFD Super Alliance | Wet Meadow | | 64.7 | 2.7 | | 6403 | HJ | |
| Saltgrass–Pickleweed NFD Super Alliance | Pickleweed–Cordgrass | Northern Coastal Salt Marsh | 0.3 | 0.0 | 0 | 6501 | HC | 52110 |
| Miscellaneous Types | | | | | | | | |
| Rock Outcrop | Barren | Mixed Barren Land | 665.3 | 376.0 | 1539.9 | 9001 | BA | 11770 |

TABLE 3. CONTINUED.

| MCV vegetation type classes | CalVeg alliance type | GAP/CNDDDB type classes | MCV mapped hectares | CalVeg mapped hectares | GAP mapped hectares | MCV type codes | CalVeg type codes | GAP CNDDDB codes |
|---|----------------------------|--|---------------------------|------------------------------|---------------------------|----------------------|-------------------------|------------------------|
| Riverine, Lacustrine and Tidal Mudflats | [Barren] | Bays and Estuaries | 82.9 | | 0 | 9002 | [BA] | 11540 |
| Serpentine Barrens | [Barren] | Streams and Canals | 17.9 | | 0 | 9003 | [BA] | 11510 |
| Human-Non-native | | | | | | | | |
| Urban or Built-up | Urban or developed | Urban or Built-Up Land | 4854.8 | 1642.9 | 752.8 | 9100 | UB | 11100 |
| Eucalyptus Alliance | Eucalyptus | Eucalyptus Groves (exotic) | 30.4 | 0.0 | 0 | 1123 | QZ | 11300 |
| | Non-native/Ornamental | | | 7.3 | | | IM | |
| | Grass Conifer/Hard-wood | | | | | | | |
| | Non-native/Ornamental | | | 171.6 | | | IG | |
| | grass | | | | | | | |
| | Non-native/Ornamental | | | 11.2 | | | IH | |
| | Hardwood | | | | | | | |
| | Non-native/Ornamental | | | 2.0 | | | IS | |
| | Shrub | | | | | | | |
| Agriculture | Agriculture | Agricultural types | 21,180.4 | 20,657.0 | 1297.7 | 9200 | AG | 11200 |
| | | Agricultural types | | | 769.5 | | | 11201 |
| | | Agricultural types | | | 4818 | | | 11210 |
| Vacant | [Barren] | | 385.0 | | | 9300 | [BA] | |
| Water | Water | Permanently-flooded Lacustrine Habitat | 8867.5 | 8571.8 | 5250.4 | 9400 | WA | 11520 |
| | | Strip Mines, Quarries and Gravel Pits | | | 10 | | | 11750 |
| Unidentified | | | 576 | | 18,225.6 | 9999 | | |

TABLE 4. SUMMARY OF VEGETATION EXTENTS. The mapped extents of MCV, CalVeg and Gap Analysis vegetation maps for a subsection of Napa county are shown here. The full list of types has been reduced to nine categories for easier comparison.

| | MCV mapped hectares | CalVeg mapped hectares | Gap mapped hectares |
|----------------------|---------------------|------------------------|---------------------|
| Hardwood types | 64,751 | 62,386 | 61,122 |
| Coniferous types | 17,549 | 19,579 | 57,350 |
| Riparian types | 2149 | 357 | 0 |
| Hard Chaparral types | 43,236 | 46,963 | 19,238 |
| Soft chaparral types | 12 | 29 | 0 |
| Grassland types | 19,015 | 22,749 | 13,134 |
| Wetland types | 137 | 3 | 0 |
| Miscellaneous | 766 | 376 | 1540 |
| Human/Non-native | 35,894 | 31,064 | 31,124 |

phyllum)) (1100), and Douglas-fir—Ponderosa Pine (*P. menziesii*—*Pinus ponderosa*) (2224), see Table 3 for corresponding CalVeg types.

Regional summary of three vegetation maps. MCV, GAP and CalVeg map similar hardwood extents (Table 4). Note that we adjusted the GAP extent from 713 km² to 611 km² due to a known error in the GAP map (David Stoms personal communication). The GAP map has 398 km² and 377 km² more coniferous vegetation than MCV or CalVeg. The MCV map of hard chaparral types is similar to CalVeg and about double the extent found in GAP. MCV soft chaparral types span half those in the CalVeg map, while none are identified in the GAP map. The MCV map identifies ~37 km² less grasslands than CalVeg and 60 km² more than GAP (Table 4).

The most significant differences between the three maps involve riparian vegetation and wetlands, which are important for wildlife habitat and landscape connectivity. Riparian types are much more widely represented in the MCV map than in CalVeg or GAP (where they are noted, but not spatially recorded). Wetlands are also better represented in the MCV map than in CalVeg or GAP (Table 4). Human land use and non-native types (excluding eucalyptus) were relatively similar (Table 4). For the small miscellaneous category, combining rock outcrops, open flowing water and serpentine barrens, GAP has twice the area of MCV or CalVeg.

DISCUSSION

Human photo interpretation produced a realistic looking, and accurate, spatial delineation at a modest increase in cost over automatic classification. Nevertheless, the new MCV map is only a first step in what will necessarily be an iterative process of plot data collection, vegetation type description and mapping using higher resolution color imagery.

MCV Map

Strengths. The MCV map's strengths include: high spatial and floristic resolution, relatively low cost, speed of production, scalability to different levels of floristic classification, hierarchical conformance with national (NVCS) standards, and the ease with which it can be crosswalked with CWHR and other widely used classification systems. The method relies on GIS data available throughout California, and much of the West, and should be easy to implement elsewhere, though local vegetation identification keys will be needed for each new region. The map is simple to relate to other digital maps since it matches the mapping scale of standard USGS maps.

The spatial resolution of any vegetation map increases as the classification proceeds from coarse physiognomic to finer floristic levels. The fine spatial resolution of the MCV map is a consequence of the 1-m pixels of the base DOQQ imagery, the relatively small MMU (<1 ha for vegetation types of conservation or management interest) and the large number of floristic types mapped. The MCV map also maintains fine spatial resolution when it is aggregated to higher physiognomic levels (12 vegetation types at the Group-Formation level; six at the Class-Subclass level).

Updates to the MCV map should be relatively easy as new imagery becomes available, since detailed re-interpretation will be needed only on polygons that have changed. Ancillary data layers such as CDF wildfire maps that identify most fire-disturbed areas, and biannual farmland monitoring maps that show conversion of natural vegetation to agriculture, will speed the interpretation and re-labeling process of a map update.

Limitations. We mention three types of limitations to the MCV map: 1) undocumented vegetation types; 2) the date of the imagery used; and 3) the capacity of the imagery to resolve some species. First, there are a large number of previously undocumented vegetation types used in the vegetation classification. California is ecologically complex, with the nation's highest diversity of plant communities (Stein et al. 2000). Broad-scale efforts to quantitatively define California's vegetation only began in earnest in the early 1990s (Sawyer and Keeler-Wolf 1995), and the MCV classification is a work in progress. The number of defined alliances has more than doubled since the first edition of the MCV was published (Keeler-Wolf personal observation). Moreover, many parts of California have not had systematic plot-based vegetation surveys. Consequently, only 44% of the MCV landcover types for Napa County are previously defined alliances, which necessitated pre-mapping field reconnaissance to identify local vegetation types and classification rules. Mapping projects can play a central role in identifying previously undefined vegetation types for inclusion. Inclusion of vege-

tation plot data collection is necessary to produce an accurate map, and to advance the classification of California's vegetation. No funds were available to support the vegetation plot data collection for our project, but we recommend such data be collected in the future.

The second limitation of the MCV map is the 1993 date of the base imagery, which makes the "new" map effectively ten years old. However, this affords the opportunity to use newer imagery to record land use changes that have occurred over the past decade.

The third limitation is the inability to identify certain dominant canopy species in the black and white DOQQ imagery. For example, it was difficult to identify the presence of Foothill Pine in the imagery when pine cover was less than 20%, due to its sparse canopy, light needles and near absence of a cast shadow. In addition, the relationship between Foothill Pine and various environmental factors including substrate, moisture and temperature relationships, is not quantitatively documented, so it was not possible to model the distribution of this species.

Similarly, many oak assemblages observed in the field were lumped into a single Mixed Oak cover type, as they were neither distinguishable in the imagery, nor easy to model without plot data. California bay and madrone were difficult to differentiate, and dominant shrub species co-occurred in such a way that it was difficult to reliably divide the shrub communities into the pre-determined classes found in the MCV. Species richness is quite high in these shrub communities. Within-stand species distribution patterns are often complex, and boundaries between shrub communities and adjacent types vary from sharp and distinct to broad and gradational. As a consequence, shrub-type labels and delineation, particularly between adjacent shrub types, was not as accurate as for forest and woodland types.

Riparian vegetation heterogeneity also posed some labeling problems. Riparian communities exhibited notable changes in dominant species composition from stream reach to stream reach, but this turnover usually occurred at scales below the target MMU and was hard to detect on the imagery. The riparian polygons in the MCV map are long, linear and seemingly homogeneous, when, in fact, many have observable changes in structure and composition along their length. Ground-based field mapping will be required to more finely map riparian cover types. Nevertheless, the photointerpretation process used in the MCV maps was clearly better able to identify riparian features than the automated procedures used to generate the CalVeg coverage.

Finally, most herb-dominated types were aggregated into coarser physiognomic classes, due to their similar appearance in the imagery. For any vegetation map, fieldwork will be necessary to map herb-dominated communities reliably at the floristic

levels of alliance or association. Despite these limitations, the MCV map was able to record the spatial distribution of 48 vegetation types.

Prospects for MCV map revision. Many of the image interpretation and classification problems could be overcome by the use of imagery with greater spectral resolution. Color imagery or hyperspectral data would likely permit many of the species ambiguities to be resolved, and would enable mappers to delineate exposed geology of floristic interest (Roberts et al. 1998). Radar and Lidar data can yield more information on stand structure (Riano et al. 2003). Satellites with higher spatial and spectral resolution should improve change-detection and our ability to estimate vegetation predictors such as soil moisture and evapotranspiration. MCV mapping methodologies can be readily applied to better imagery as it becomes available.

A more detailed geology map (than 1:250,000) and a more current farmlands data layer would help the next iteration of the map. All other data used were available at scales of 1:24,000 or 1:12,000, including a soils map (U.S. Dept Agriculture 2000), which showed serpentine specific soils at the resolution of the DOQQ's. The MCV map could also be modified to provide an Anderson level II subdivision (Anderson et al. 1998) of agricultural types using the California Division of Land Resource Protection FMMP maps, which would permit use of the revised CWHR classification.

Spatial extent, commonness, rarity and conservation application. Patterns of spatial extent (Table 1, Fig. 2) provide insights into the utility of the MCV map for various planning and conservation purposes. In Napa County, the 10–15 vegetation types of greatest spatial extent cover 70–80% of the natural landscape and form the matrix of the observed landscape. The rarest 50% of the vegetation classes comprise, in aggregate, only 5% of the county's total area. These results can be used in conservation planning, whether for biodiversity, scenic open space or working landscapes. Given the map scale, analyses are possible on a watershed or finer basis.

Map Comparisons

Number and size of polygons. Comparing polygon size distribution allows for an estimation of landscape complexity captured by the maps. Where equal vegetation type extents were measured between GAP and MCV, MCV provides more information about the distribution. MCV and CalVeg have an equal number of polygons, but the smaller polygons in the MCV permit capture of ecological information below the resolution of the CalVeg map.

Classification comparison. The MCV map had greater floristic detail, particularly for riparian and grassland types, with five and four categories com-

pared with three and one for CalVeg and zero and two for GAP. CalVeg identified one type that was not detected in the current MCV map.

Each of the classification systems has vegetation types used to aggregate difficult species combinations into coarser units within the classification hierarchy. These types represent vegetation combinations that have not been separated out, or are beyond the resolution of the imagery to differentiate. MCV has Winter-Rain Sclerophyll Forests and Woodlands and Mixed Oak. CalVeg aggregates multiple species into Mixed Hardwood, Productive Mixed Hardwoods, Gray Pine, and Mixed Conifer Pine. GAP's aggregated types include Coast Range Mixed Coniferous Forest (which does not cross-walk to MCV), Mixed Evergreen Forest, and Mixed North Slope Cismontane Woodland. One of the differences between the classification systems is that those vegetation types still under development are clearly identified in the MCV classification through the use of the term 'Not Formally Defined' (NFD) to identify types that still need additional fieldwork. In that sense, the MCV is explicit about the iterative process that all vegetation classification systems go through as additional data are added.

The CalVeg classification scheme generally identifies fewer species in a given polygon than the MCV map does. Both MCV and CalVeg classifications have many species identified as possible alliance components (Sawyer and Keeler-Wolf 1995; Schwind and Gordon 2001). Generally, the MCV map provides more information about sub-dominants and low cover percentage co-dominants than does CalVeg. GAP compares favorably to the other two in terms of identifying up to three dominant species in any given vegetation type, but there is little information on associated sub-dominants.

Minimum mapping units and polygon size. The variable lower limit on polygon size in the MCV map allows vegetation analysts and conservation planners a method of selectively delineating features of particular conservation interest, such as seeps, without an impossible increase in mapping costs on common vegetation types.

Imagery. In CalVeg, vegetation is classified for each 30-m pixel (900 m²), then aggregated to 1 ha, versus 1 m² resolution and a 0.25 ha MMU for MCV. Both CalVeg's line work and its classification are driven by multiple automated, rule-based algorithms, which account for its pixilated appearance (Fig. 3b). The MCV line work more closely resembles the sinuous nature of natural vegetation breaks (Fig. 3a), because the polygons are delineated by hand over high-resolution imagery (Fig. 3d). MCV polygons may not be as repeatable because of being hand-drawn. However, the detail in the MCV map is comparable to CalVeg, and its variable MMU permits the registration of many stands not delineated by to CalVeg.

The interaction between spatial accuracy and flo-

ristic labeling accuracy is a factor that we did not measure in this project. At issue is the question of whether very small polygons are well enough spatially positioned so that their attributes actually refer to the intended vegetation. The level of registration accuracy in the CalVeg and MCV maps is an open question, one that we feel warrants further study. GAP polygons, being generalized, would not be considered potentially inaccurate in this way.

The GAP map (Fig. 3c) is the most spatially general map, with a mean polygon size of approximately 3072 ha in Napa County. The GAP polygons were hand-delineated using TM imagery as the backdrop; so GAP map linework more naturally reflects breaks in vegetation than the CalVeg map. However, since the CalVeg map has finer spatial resolution, but uses the same TM imagery, it better identifies dominant vegetation on a pixel-by-pixel basis.

Note that the CalVeg, GAP and MCV classifications all contain stand structure information not analyzed here, and that adjacent polygons may contain the same vegetation, differing only on the basis of plant size or cover attributes.

Vegetation extent comparisons. By combining vegetation types into more abstracted hierarchical classes, we identified some of the overall differences between the three maps (Table 4). Hardwoods are fairly evenly mapped between the three maps. MCV and CalVeg identified similar levels of conifers (~200 km²), but the GAP map had nearly three times as much conifer area. The GAP map under-reports chaparral in the region by about 200 km², compared to the other maps. This suggests that the GAP classification bins chaparral types into conifer types. Conifers in the MCV map are about 20% percent lower than CalVeg, which may represent the mis-classing of low density foothill pine into chaparral types.

Grassland types were roughly equivalent in extent between MCV and CalVeg at about 200 km² in the county. GAP reports this class at about 130 km². The difference is likely due to low cover stands of hardwood and conifer- that might be classed as grasslands by MCV and CalVeg- being classed as Woodland types in GAP. At the scale GAP is working, this type of classification is justifiable, since it is more conservative to register a low-cover stand as woodland than as grassland from a resource management perspective. In the California Coast Range, many grasslands are openings in a woodland matrix, and thus are appropriately lumped into woodland at GAP's scale of spatial aggregation. Another possible explanation is that in the approximately 10 years between the imagery used for GAP (1990 Landsat TM) or MCV (1993 DOQQ's) and CalVeg (recent Landsat TM), many of the low density woodlands of Napa may have been converted to grassland.

The MCV map identified considerably more ri-

parian and wetland areas than either of the other maps. Considering the high ecological value of these types, this marks one of the most valuable contributions the MCV map can make to the management of lands in Napa County. Valley oak, both as a member of riparian areas and as its own alliance, is better mapped by MCV than the other maps. MCV identifies about three times as much valley oak as GAP, and four times the amount mapped in CalVeg. MCV also identifies rock outcrops, not classed in the other systems. Rock outcrops are habitat for many rare species that may not occur frequently enough to form an alliance.

All three maps identified similar extents for human and non-native cover types. This is unusual, since it is known that there has been extensive vineyard conversion between the dates the maps were made. MCV identifies about 40 km² more than the other two, despite its older base map imagery compared to CalVeg. The difference may be due to the finer scale of mapping, which could identify human altered landscapes on smaller areas than the other maps.

Future research and applications. Conservation planning on a species by species basis can be complicated by the large numbers imperiled species. Conservation for groups of species (Grossman et al. 1998) and preservation of natural vegetation types in an ecoregional context is increasingly important. When protected, natural vegetation types help to conserve their component species, both rare and common (e.g., GAP logic, Davis et al. 1998). The MCV map vegetation types can be used in developing a comprehensive conservation design for the county. The authors recommend that the map be used in conjunction with ancillary data sources for conservation planning (Noss et al. 1997; Thorne et al. 2002; Thorne 2003).

The MCV map is useful for a wide array of natural resource management purposes, including forest and range inventory and assessment, watershed characterization in support of hydrologic modeling and erosion control, wildfire risk and behavior modeling, urban-wildland interface issues, and disease risk and spread modeling. This latter use is of particular importance, since the majority of species susceptible to Sudden Oak Death Syndrome (SODS) caused by the fungus, *Phytophthora ramorum*, are canopy dominant species that form the basis for defining many MCV alliances and map units. Therefore, the new map is especially suitable for SODS risk assessment and spread analysis.

Other applications include land use planning and policy assessment and pre-project impact scoping. Finally, the map can be used to identify and target areas for more detailed ground-based vegetation inventory and mapping work.

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ALLOZYME VARIABILITY WITHIN AND AMONG VARIETIES OF
ISOMERIS ARBOREA (CAPPARACEAE)

HAROLD D. TRUESDALE¹, LEROY R. MCCLENAGHAN JR., BOYD D. COLLIER,
AND KATE BURMEISTER

Department of Biology, San Diego State University, San Diego, CA 92182

KEVIN J. RICE

Department of Agronomy and Range Science, University of California,
Davis, CA 95616

ABSTRACT

The pattern of genetic variation within and among 13 natural populations (294 individuals) representing the four varieties of *Isomeris arborea* (Capparaceae) throughout its range in California was investigated with allozyme electrophoresis. Thirty enzyme loci were examined. Low genetic diversity within populations ($A = 1.18$, $P = 0.139$, $H_E = 0.051$ and $H_O = 0.051$) and significant genetic differentiation among populations ($F_{ST} = 0.462$) were found. A relatively large number of private alleles (9) were detected as well as several unique alleles confined to single varieties. We found a relatively high proportion of total genetic diversity (45%) among varieties and a significant correlation ($P < 0.001$) between F_{ST} and geographic distance. Multiple regression analyses demonstrated clines in genetic diversity measures, from East to West and South to North. Multiple Correspondence Analysis (MCA) clearly demonstrated division into a minimum of two groups. The above observations together with low gene flow estimates suggest genetic drift by isolation may have been critical to the current genetic structure of the species. We tentatively argue, based on our results, that variety *globosa* may be deserving of subspecies status.

Key Words: *Isomeris arborea*, genetic structure, Capparaceae, gene flow, bladder pod.

Almost all species exhibit some degree of spatial genetic heterogeneity (Avice 1994). While spatial genetic structure can result from several processes, in plant species the amount of gene flow is pivotal in determining the distribution of genetic variation (Loveless and Hamrick 1984; Hamrick and Godt 1990). Gene flow in plant species can be highly localized (Endler 1977) as well as temporally and spatially variable (Govindaraju 1989; Ellstrand 1992). Restriction of gene flow by limited seed and/or pollen dispersal might produce isolation by distance with subsequent differentiation among groups by genetic drift. Spatial genetic structure can also reflect an interaction between environmental factors that are spatially and/or temporally dynamic and various life-history characteristics (Slatkin 1985; Hamrick and Godt 1990, 1996; Boyle et al. 1990; Perry and Knowles 1991; Knowles et al. 1992). For example, the interaction of reproductive dynamics and disturbance (decreased fire frequency intervals) may account for some of the genetic structure found in *Cupressus forbesii* (Truesdale and McClenaghan 1998). The distribution of genotypes within and among populations may also be affected by selection with patterns of differentiation reflecting spatially varying selective regimes. Species which occupy an array of habitats among which dispersal is limited may exhibit local adaptation

(Slatkin 1985) and isolation-by-distance even in the absence of spatially varying selection (Wright 1951; Endler 1977).

Isomeris arborea Nutt. (= *Cleome isomeris* E. Greene; Capparaceae) is a drought-deciduous, perennial shrub endemic to southern California and Baja California, Mexico, where it grows in several habitats from the coast to the desert. Commonly called bladderpod, *I. arborea* is a monotypic genus (Vanderpool 1993) consisting of four varieties: *I. arborea* var. *arborea* (coastal), *I. arborea* var. *angustata* Parish (desert), *I. arborea* var. *globosa* Cov. (Tehachapi Mountains) and *I. arborea* var. *isularis* Jepson (southern Channel Islands). These varieties, hereafter referred to as *arborea*, *angustata*, *globosa* and *insularis*, are recognized primarily on the basis of fruit morphology, which appears to be loosely correlated with geography (Vanderpool 1993; Truesdale personal observation). Fruits are dehiscent, photosynthetic, contain a conspicuous inner gas space, and contribute significantly to the carbon economy of the plant and developing seed (Goldstein et al. 1990). *Isomeris arborea* is andromonoecious, producing both male and hermaphroditic flowers on the same plant. Flower visitation by insects is high (Truesdale personal observation). Little recruitment within populations is observable but may occur episodically. Seeds are heavily preyed upon by a variety of rodent species (Niccoli 1987), are relatively heavy and not readily dispersed. The species is not a true xerophyte, being unable to tolerate the low soil water potentials typically found

¹ Author for correspondence, email: htruesda@sunstroke.sdsu.edu

in the desert, but is apparently able to access perched ground water under sandy washes and depressions with its deep, rapidly growing tap-root system (Goldstein et al. 1990).

Stebbins and Major (1965) have suggested that *I. arborea* was a member of the Madro-Tertiary Geoflora and list it as a paleoendemic. Iltis (1957) places *Isomeris* in *Cleome* sect. *peritoma* based on morphological characteristics. While the geographic origin of *Cleome* is unknown, Axelrod (1948) suggests that the important distribution center was the Mexican highlands. The overall distribution of the genus *Cleome* parallels the present-day distribution of the Madro-Tertiary flora, is most probably of mesophytic origin and is proposed as having initially developed pre-Eocene (Axelrod 1958; Raven and Axelrod 1978). The northward migration of the Madrean vegetation from southwestern North America, which began during the Pleiocene, and radiated northwestwardly into semi-arid areas of the western United States may account for some of the differentiation found in the genus (Raven and Axelrod 1978). During the late Pleiocene, orogenic activity led to formation of the Sierra, Transverse and Coastal Ranges as well as the formation of the Great Basin and Southwestern deserts, and the current desert flora of southern California developed from the Madro-Tertiary Geoflora (Axelrod 1948, 1958). The distribution of modern desert species is proposed by Raven and Axelrod (1978) to have been primarily shaped by the extreme topographic, edaphic and climatic diversity associated with fluctuations in climate in conjunction with dynamic geologic change. The spread of warmer, drier climate since the Xerothermic enabled taxa existing in semi-desert sites to spread to the southern California coast and the Channel Islands (Raven and Axelrod 1978).

Johnson (1968), in contrast, has proposed that *I. arborea* was a desert colonizer, with coastal populations being much older than desert populations and pre-adapted to dry habitats, having developed in a much earlier, much drier coastal environment. As deserts formed in the late Pleistocene, *I. arborea* was able to invade and survive the arid conditions as a result of pre-adaptations.

Gittins (1965) has proposed that the formation of the Transverse Ranges separated *globosa* from the desert variety and allowed the fixation of the extreme globose form of seed capsule in this area through isolation and subsequent genetic drift. Variety *insularis* occurs naturally only on the Southern Channel Islands, which are of Mexican origin (Schoenherr 1992).

We had several goals in this study. We wanted to describe the population genetic structure among *I. arborea* populations. With the exception of *globosa* there is little morphological divergence among varieties. This suggests that 1) the region, as a whole, has been more recently colonized than proposed and populations have not had sufficient time

to develop unique traits that would warrant species designation, 2) the species is a paleoendemic but sufficient gene flow exists to maintain genetic and phenotypic cohesiveness or alternatively, 3) significant genetic divergence among populations may exist that does not correlate with phenotypic divergence. When morphological variation contains little information as in *I. arborea*, molecular evidence is particularly useful in illuminating population structure. We also wanted to ascertain whether a cline of reduced genetic variability along one or the other putative paths of colonization could be detected as current genetic structure may reflect past migration in organisms with relatively long generation times (Newton et al. 1999). In addition, Gittens' (1965) hypothesis regarding the origin of *globosa* through isolation and subsequent genetic drift suggested that genetic variation in *globosa* should be significantly lower than in other varieties.

MATERIALS AND METHODS

Leaf tissue representing the four varieties of *Isomeris arborea* was collected from 13 localities within California (Table 1). Populations sampled represent a mixture of localities originally sampled by Gittens (1965) which were still extant, and populations used in other studies by one of us (BDC). Tissue was transported to the lab on ice, stored at 4°C and extracted within 24 hours of collection. Approximately 0.5 g of leaf tissue was homogenized in an 1.5 ml Eppendorf tube with freshly prepared 0.2 M phosphate buffer (pH 7.5) containing 0.20 M sodium tetraborate, 0.01 M sodium metabisulfite, 0.015 M diethyldithiocarbamic acid sodium salt, 2% (w/v) L-ascorbic acid sodium salt, 2% (w/v) PVP-40, 0.5% (v/v) 2-mercaptoethanol and 10 mg/25 ml NADP.

Crude extracts were absorbed onto filter paper wicks and placed into 12% horizontal starch gels composed of the following buffers: lithium hydroxide: pH 8.3, histidine-citrate: pH 6.2, and tris-ver-sene-borate: pH 8.6 (May 1994). A total of 30 loci could be reliably scored of which 10 were polymorphic: non-enzymatic general protein (GP 3); β -esterase (Est, E.C. 3.1.1.1); glucose-6-phosphate isomerase (Pgi 2, E.C. 5.3.1.9); isocitrate dehydrogenase (Idh, E.C. 1.1.1.42); malic enzyme (Me, E.C. 1.1.1.40); menadiene reductase (Mnr 1,2, E.C. 1.8.1.4); peroxidase (Per 2, E.C. 5.3.1.9); phosphogluconate dehydrogenase (6PgD 2, E.C. 1.1.1.44); phosphoglucomutase (Pgm 1, E.C. 5.4.2.2).

The largest sample (Monument Road) was chosen as the reference population due to the large number of alleles (8) present at the β -esterase locus, and individuals of known electrophoretic mobility from this population were included on all gels to facilitate scoring.

Allele frequencies were calculated using Biosys-1 (Swofford and Selander 1981). Genetic variability parameters estimated included the mean number of

TABLE 1. LOCATION DATA: POPULATION NAME, POPULATION DESIGNATION, ALTITUDE AND SAMPLE SIZE FOR THE 13 POPULATIONS ANALYZED FOR GENETIC VARIATION IN *ISOMERIS ARBOREA*. Population designations refer to capsule type: A = *arborea*; G = *globosa*; T = *angustata*; I = *insularis*.

| Population name | Population designation | Location lat, long | Altitude (m) | n |
|---------------------|------------------------|-------------------------|--------------|----|
| Monument Road | A1 | 32°32.54'N, 117°06.28'W | 13 | 30 |
| Otay Mesa | A2 | 32°32.88'N, 116°59.40'W | 60 | 28 |
| Sorrento Valley | A3 | 32°54.07'N, 117°13.18'W | 15 | 20 |
| Christianitos Road | A4 | 33°24.12'N, 117°35.39'W | 280 | 20 |
| Gorman | G1 | 34°47.59'N, 118°50.56'W | 1228 | 20 |
| Oildale | G2 | 35°31.95'N, 118°58.32'W | 327 | 20 |
| Cache Creek | G3 | 35°07.84'N, 118°13.96'W | 1111 | 20 |
| Caliente Creek Road | G4 | 35°17.22'N, 118°37.56'W | 486 | 20 |
| Mecca | T1 | 33°36.45'N, 115°50.06'W | 305 | 25 |
| Cabazon | T2 | 33°55.10'N, 116°45.50'W | 500 | 28 |
| Amboy | T3 | 34°34.69'N, 115°50.02'W | 415 | 20 |
| Joshua Tree | T4 | 33°43.25'N, 115°49.52'W | 920 | 21 |
| San Clemente Island | I1 | 33°00.54'N, 118°23.28'W | 314 | 22 |

alleles per locus (A), percentage polymorphic loci (P), the observed heterozygosity (H_O) and expected heterozygosity (H_E). Conformity to Hardy-Weinberg expectations was determined by the exact test proposed by Guo and Thompson (1992) with the overall significance for each locus estimated by Fisher's combined probability test (Fisher 1970) using the GENEPOP program (version 2; Raymond and Rousset 1995). Levels of intervarietal divergence in these measures were compared by unpaired two-tailed t-tests using a Welch-Satterthwaite correction (homogeneity of variance not assumed).

Unbiased estimates of Wright's F-statistics were calculated according to the methods of Weir and Cockerham (1984) using FSTAT (version 2.9.1; Goudet 2000). F_{IS} and F_{IT} measure the correlations between two uniting gametes relative to the subpopulation and total population respectively, while F_{ST} measures the correlation between two gametes randomly drawn from subpopulations and is a measure of the degree of genetic differentiation of subpopulations. Standard errors for single locus estimates of F-statistics were calculated by jackknifing over populations, and 95% confidence intervals of multilocus estimates were calculated by bootstrapping over loci (Weir 1990). The significance of population differentiation was estimated by permuting genotypes among samples using 15,000 randomizations of the data. Wherever necessary, the significance level of each analysis was adjusted by taking into account the number of multiple tests of the same hypothesis using the sequential Bonferroni method (Holm 1979). Values of gene diversity parameters (Nei and Chesser 1983) were also calculated using FSTAT and hierarchically subdivided (Chakraborty 1980) to allow comparison to other studies.

The private alleles method (Slatkin 1985; Slatkin and Barton 1989) was used to estimate gene flow. Differentiation among subpopulations, F_{ST} , is pro-

duced by genetic drift, and countered by gene flow. Isolation by distance was analyzed by regressing pairwise estimates of F_{ST} vs. geographic distance among populations. Statistical significance was determined by Mantel analyses (Mantel 1967) using randomization testing (10,000 randomizations). Multiple regression analyses were performed on population level genetic diversity estimates using latitude, longitude and elevation as independent variables. Genetic diversity estimates (dependent variables) representing proportions (H_E , P) were arcsine transformed prior to analysis.

We also carried out a multiple correspondence analysis (MCA) with the Ecological Data Analysis software package (ADE 4; Guinand 1996), which allowed the data for individual populations to be viewed on a general factorial plane. This ordination technique, which measures correlations between the presence and absence of alleles within a contingency table, was utilized to analyze the data for the existence of complex spatial geographic clusters. The ADE 4 package was also used to determine the contribution of each axis to the total variance.

RESULTS

Of the 30 putative loci scored in this study, 10 (33%) were polymorphic in at least one population (Table 2). Of the 31 alleles detected, 9 (29%) were restricted to single populations at relatively high frequencies (mean = 0.272, range 0.100 to 0.614). Furthermore, several allelic variants were confined to a single variety, though none of these were fixed. There was no significant departure from Hardy-Weinberg expectations at any locus or significant correlation with sample size for any genetic measure.

Average number of alleles per locus (A) ranged from 1.07 at A3 to 1.30 at T1 and T3, percentage of polymorphic loci (P) from 6.67% (A3) to 20.00% (T1, T2, T4) and gene diversity (H_E) from

TABLE 2. ALLELE FREQUENCIES AT 10 POLYMORPHIC LOCI IN *ISOMERIS ARBOREA* POPULATIONS. Population designations are given in Table 1. Frequencies in bold text with underscoring indicate private alleles. Those confined to one varietal type are in italics and bold text.

| Locus | Allele | Population | | | | | | | | | | | | |
|-------|--------|--------------|--------------|-------|-------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| | | A1 | A2 | A3 | A4 | G1 | G2 | G3 | G4 | T1 | T2 | T3 | T4 | I1 |
| Est B | 1.27 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.405 | 0.000 |
| | 1.15 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | <u>0.000</u> | 0.341 |
| | 1.09 | 0.000 | 0.304 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | <u>0.000</u> |
| | 1.00 | 0.350 | <u>0.393</u> | 0.475 | 0.325 | 1.000 | 1.000 | 1.000 | 1.000 | 0.660 | 0.679 | 0.675 | 0.214 | 0.525 |
| | 0.94 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.190 | 0.000 |
| | 0.85 | 0.550 | 0.304 | 0.525 | 0.675 | 0.000 | 0.000 | 0.000 | 0.000 | 0.200 | 0.214 | 0.275 | <u>0.143</u> | 0.114 |
| | 0.79 | 0.100 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| | 0.70 | <u>0.000</u> | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.140 | 0.107 | 0.050 | 0.048 | 0.000 |
| Per 2 | 1.00 | 1.000 | 1.000 | 1.000 | 0.825 | 0.075 | 0.000 | 0.000 | 0.000 | 0.620 | 0.593 | 0.525 | 0.548 | 1.000 |
| | 0.90 | 0.000 | 0.000 | 0.000 | 0.175 | 0.925 | 1.000 | 1.000 | 1.000 | 0.360 | 0.357 | 0.350 | 0.405 | 0.000 |
| | 0.75 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.020 | 0.050 | 0.125 | 0.048 | 0.000 |
| Pgi 2 | 1.13 | 0.000 | 0.000 | 0.000 | 0.000 | 0.550 | 0.600 | 0.425 | 0.700 | 0.020 | 0.018 | 0.000 | 0.024 | 0.000 |
| | 1.00 | 1.000 | 1.000 | 1.000 | 1.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.980 | 0.982 | 1.000 | 0.976 | 1.000 |
| | 0.75 | 0.000 | 0.000 | 0.000 | 0.000 | 0.450 | 0.400 | 0.575 | 0.300 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Pgm 1 | 1.00 | 0.983 | 1.000 | 1.000 | 1.000 | 0.500 | 0.575 | 0.650 | 0.850 | 0.980 | 0.982 | 0.925 | 0.976 | 1.000 |
| | 0.93 | 0.017 | 0.000 | 0.000 | 0.000 | 0.450 | 0.400 | 0.325 | 0.100 | 0.020 | 0.018 | 0.075 | 0.024 | 0.000 |
| | 0.84 | 0.000 | 0.000 | 0.000 | 0.000 | 0.050 | 0.025 | 0.025 | 0.050 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Mr 1 | 1.00 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.773 |
| | 0.88 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.227 |
| Mr 2 | 1.00 | 1.000 | 0.821 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | <u>1.000</u> |
| | 0.50 | 0.000 | 0.179 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Idh | 1.10 | 0.000 | <u>0.000</u> | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.614 |
| | 1.00 | 0.950 | 0.946 | 1.000 | 1.000 | 0.900 | 0.900 | 0.500 | 0.450 | 0.450 | 0.120 | 0.679 | 0.200 | 0.095 |
| | 0.80 | 0.050 | 0.054 | 0.000 | 0.000 | 0.100 | 0.500 | 0.550 | 0.550 | 0.880 | 0.321 | 0.800 | 0.905 | 0.114 |
| Gp 3 | 1.17 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.060 | 0.071 | 0.000 | 0.405 | 0.000 |
| | 1.00 | 0.750 | 1.000 | 1.000 | 0.100 | 1.000 | 1.000 | 1.000 | 1.000 | 0.600 | 0.607 | 0.550 | 0.595 | 0.568 |
| | 0.80 | 0.250 | 0.000 | 0.000 | 0.900 | 0.000 | 0.000 | 0.000 | 0.000 | 0.340 | 0.321 | 0.450 | 0.000 | 0.432 |
| 6-Pgd | 1.00 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 0.875 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| | 0.90 | 0.000 | 0.000 | 0.000 | 0.00 | 0.000 | 0.000 | 0.125 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |
| Me | 1.00 | 1.000 | 1.000 | 0.925 | 1.000 | 1.000 | 1.000 | <u>1.000</u> | 0.725 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |
| | 0.82 | 0.000 | 0.000 | 0.075 | 0.000 | 0.000 | 0.000 | 0.000 | 0.275 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |

0.022 at A3 to 0.068 at T4 (Table 3). Gene diversity (H_E) was significantly lower in *arborea* than *globosa* ($t = -4.8167$, $P = 0.0044$) or *angustata* ($t = -9.0811$, $P = 0.00079$). For the measures A and P, *arborea* was significantly lower than *angustata* ($P = 0.0036$ and 0.0022 respectively) but comparisons to *globosa* were non-significant ($P = 0.24$ and 0.18 respectively).

The mean value of F_{ST} over all loci and populations is 0.462, indicating substantial genetic differentiation (Table 4). Allele frequencies differ significantly among populations by an exact test ($P < 0.0001$), and multilocus genotypes differed markedly among varieties. Intravarietal F_{ST} estimates were significant ($P < 0.01$) in *arborea* ($F_{ST} = 0.285$) and *angustata* ($F_{ST} = 0.098$), but not *globosa* ($F_{ST} = 0.082$). Permutation testing of pairwise estimates of F_{ST} within varieties displayed similar significance.

Average gene diversity values were: $H_T = 0.276$, $H_S = 0.152$, $D_{ST} = 0.124$ and $G_{ST} = 0.449$. Hierarchical analysis revealed that D_{ST} was divided into D_{SV} (gene diversity among populations within varieties) = 0.021 and D_{VT} (gene diversity among varieties) = 0.103. Therefore, 7.5% of the total ge-

netic diversity could be accounted for by variation among populations within varieties, 37.4% by variation among varieties and 55.1% by variation within populations.

The estimate of N_m was 0.125 from the private alleles method of Slatkin (1985). Intravarietal estimates were consistent with the above for *arborea* ($N_m = 0.388$), but inconsistent for *angustata* and *globosa* (both $N_m > 1.0$). Mantel analysis between pairwise F_{ST} values and geographic distances (km) revealed that a clear association exists between these two variables ($P < 0.001$ for 10,000 randomizations).

Multiple regression analysis on the 12 mainland populations of *I. arborea* revealed that gene diversity (H_E) was significantly correlated with both latitude and longitude. A significant decline in population levels of diversity was indicated from east-to-west, and a significant increase from south-to-north (Table 5). Mean number of alleles per locus and percentage polymorphic loci displayed the same significant association for longitude but not latitude. No dependent variable was correlated with elevation.

TABLE 3. GENETIC VARIABILITY MEASURES: OBSERVED HETEROZYGOSITY (H_o); GENE DIVERSITY (H_e); MEAN NUMBER OF ALLELES PER LOCUS (A); PERCENT POLYMORPHIC LOCI (P) AND SAMPLE SIZE (n) FOR *ISOMERIS ARBOREA* POPULATIONS. All estimates of variability measures are based on all 30 loci scored with standard errors in parentheses. Means for variability measures are weighted with standard deviations in parentheses. Population abbreviations are given in Table 1.

| Population | H_o | H_e | A | P (99%) | n |
|------------|---------------|---------------|-------------|-----------|-----|
| A1 | 0.036 (0.022) | 0.036 (0.023) | 1.17 (0.08) | 13.33 | 30 |
| A2 | 0.035 (0.024) | 0.036 (0.024) | 1.13 (0.08) | 10.00 | 28 |
| A3 | 0.021 (0.017) | 0.022 (0.018) | 1.07 (0.05) | 6.67 | 20 |
| A4 | 0.030 (0.018) | 0.031 (0.018) | 1.10 (0.06) | 10.00 | 20 |
| G1 | 0.045 (0.025) | 0.046 (0.025) | 1.17 (0.08) | 13.33 | 20 |
| G2 | 0.050 (0.028) | 0.051 (0.028) | 1.13 (0.08) | 10.00 | 20 |
| G3 | 0.056 (0.028) | 0.057 (0.028) | 1.17 (0.08) | 13.33 | 20 |
| G4 | 0.050 (0.025) | 0.051 (0.026) | 1.13 (0.06) | 13.33 | 20 |
| T1 | 0.060 (0.028) | 0.061 (0.029) | 1.30 (0.12) | 20.00 | 25 |
| T2 | 0.066 (0.030) | 0.067 (0.030) | 1.27 (0.11) | 20.00 | 28 |
| T3 | 0.065 (0.029) | 0.066 (0.030) | 1.20 (0.09) | 16.67 | 21 |
| T4 | 0.066 (0.033) | 0.068 (0.033) | 1.30 (0.13) | 20.00 | 21 |
| II | 0.065 (0.031) | 0.067 (0.032) | 1.20 (0.10) | 13.33 | 22 |
| Means | 0.050 (0.015) | 0.051 (0.015) | 1.18 (0.07) | 13.85 | 23 |

Axis 1 of the MCA projection (Fig. 1) clearly distinguishes *globosa* from other varieties and explains approximately 62% of the variance in allele frequencies. Three clusters related to pod type are indicated: the first consists of all *globosa* populations, the second of all *arborea* populations and the third of *angustata* populations T1, T2, and T3. Population T4 contains two private alleles and differs markedly in frequency from other *angustata* populations at several loci. Population II contains three unique alleles at high frequencies (range: 0.614–0.227).

DISCUSSION

Our results show a significant reduction in gene diversity and number of alleles in *arborea* (coastal) populations. Widespread loss of alleles and increased homozygosity is a general expectation from repeated founder events along a path of range expansion (Hewitt 1996, 1999). Multiple regression

analyses indicate significant east-to-west and south-to-north clines in genetic diversity measures. All measures of variation show *angustata* populations to be genetically more diverse compared to *arborea* and *globosa* populations.

In contrast, we detected a number of private alleles at high frequency and unique alleles confined to single varietal types. Furthermore, there is relative intravarietal homogeneity but high intervarietal differentiation. This indicates these varieties have been genetically separated for a substantial period of time, implies that this species may now be in the process of speciation and is characteristic of relict populations (Slatkin 1993).

We conclude that these patterns are more supportive of Axelrod's (1948, 1958) interpretation of the history and development of the Madro-Tertiary Flora as displaying a radial pattern of spread over southwestern North America in response to climatic and geologic change. As orogenic activity and

TABLE 4. F-STATISTICS (WEIR AND COCKERHAM 1984) FOR TEN ELECTROPHORETIC LOCI SURVEYED IN 13 POPULATIONS OF *ISOMERIS ARBOREA* FROM CALIFORNIA. Standard errors of the jackknifed estimates over populations are given in parentheses. Means are jackknifed estimates over loci with 95% bootstrap confidence intervals in parentheses below. Significance of population differentiation was determined by 15,000 randomizations of genotypes among samples. *** $P < 0.0001$.

| Locus | F_{IS} | F_{IT} | F_{ST} |
|-------------|----------------|---------------|------------------|
| Est β | 0.123 (0.041) | 0.357 (0.053) | 0.267 (0.059)*** |
| Per 2 | 0.043 (0.068) | 0.643 (0.143) | 0.625 (0.141)*** |
| Pgi 2 | 0.086 (0.089) | 0.713 (0.040) | 0.686 (0.028)*** |
| Pgm 1 | 0.017 (0.166) | 0.281 (0.096) | 0.275 (0.053)*** |
| Mr 1 | 0.283 (0.136) | 0.479 (0.229) | 0.229 (0.109)*** |
| Mr 2 | 0.105 (0.113) | 0.549 (0.114) | 0.492 (0.090)*** |
| Idh | -0.102 (0.066) | 0.314 (0.190) | 0.373 (0.148)*** |
| Gp 3 | -0.013 (0.088) | 0.201 (0.155) | 0.211 (0.109)*** |
| 6-Pgd | 0.643 (0.309) | 0.770 (0.370) | 0.191 (0.092)*** |
| Me | 0.183 (0.151) | 0.467 (0.276) | 0.307 (0.151)*** |
| Mean | 0.062 | 0.495 | 0.462*** |
| | (-0.013-0.111) | (0.342-0.608) | (0.314-0.580) |

TABLE 5. MULTIPLE REGRESSION ANALYSIS OF LATITUDE, LONGITUDE AND ELEVATION ON EXPECTED HETEROZYGOSITY (H_E), MEAN NUMBER OF ALLELES PER LOCUS (A) AND PERCENTAGE POLYMORPHIC LOCI (P) FOR 12 MAINLAND *ISOMERIS ARBOREA* POPULATIONS. The r^2 values provided are adjusted for sample size.

| Variable | Slope | SE | t | P |
|---|---------|--------|--------|-------|
| Dependent variable = Expected heterozygosity ($r^2 = 0.775$) | | | | |
| Latitude | 1.497 | 0.391 | 3.824 | 0.005 |
| Longitude | -1.393 | 0.321 | -4.325 | 0.003 |
| Elevation | 0.001 | 0.001 | 1.285 | 0.235 |
| Constant | 124.594 | 34.069 | 3.657 | 0.005 |
| Dependent variable = Mean number of alleles per locus ($r^2 = 0.640$) | | | | |
| Latitude | 0.012 | 0.021 | 0.570 | 0.584 |
| Longitude | -0.051 | 0.015 | -3.936 | 0.010 |
| Elevation | 0.050 | 0.031 | 0.447 | 0.142 |
| Constant | 7.165 | 1.531 | 4.670 | 0.005 |
| Dependent variable = Percentage polymorphic loci ($r^2 = 0.623$) | | | | |
| Latitude | 1.248 | 0.888 | 1.406 | 0.197 |
| Longitude | -2.718 | 0.727 | -3.739 | 0.006 |
| Elevation | 0.003 | 0.002 | 1.562 | 0.157 |
| Constant | 296.514 | 77.244 | 3.839 | 0.006 |

marked seismic events led to a diversification of topography, new, more localized habitats developed in the southwest (Axelrod 1948, 1958). Dramatically fluctuating Pleistocene climate changes impacted these environments (Axelrod 1948). The influence of these highly variable, narrowly localized environments continued into the Holocene (Cole and Wahl 2000) and may explain some of the diversification found in *I. arborea*.

Our results also show a strong pattern of increasing F_{ST} with increasing geographic distance among the populations studied and a high degree of genetic divergence among populations regionally. Gene flow estimates from private alleles ($N_m = 0.125$) indicate that the number of migrants per generation is insufficient to preserve genetic cohesiveness. Furthermore, hierarchical analysis of population subdivision indicated that more cohesiveness exists within rather than between varieties, and that varieties were differentiated into more or less separate groups by the MCA (Fig. 1).

Variety *globosa* is characterized by two unique alleles that occur in all sampled populations (Table 2). This variety is, likewise, monomorphic at the β -esterase locus (fixed for the most common allele), which is highly polymorphic in other varieties. The MCA (Fig. 1) clearly delineates *globosa* from other varieties. Comparisons of patterns of genetic vari-

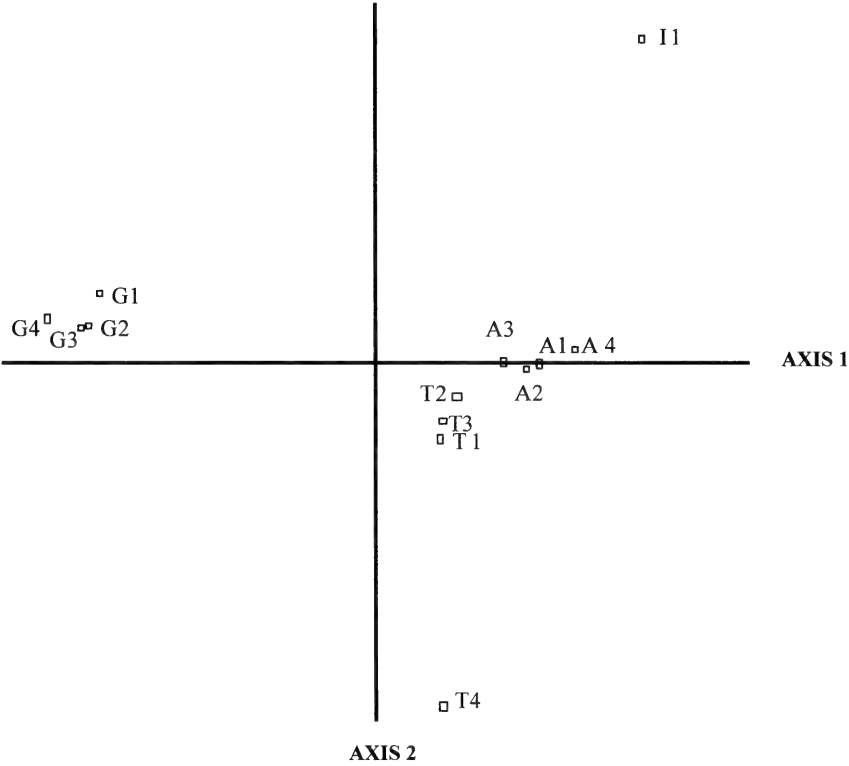


FIG. 1. Multiple Correspondence Analysis (MCA) of allele frequencies in *Isomeris arborea* populations. Variety *globosa* is clearly distinguishable by axis 1 which explains 62% of the variance. Axis 2 clusters the other varieties surveyed and explains 10% of the variance in the data. Population designations are given in Table 1.

ability in *globosa* with those in *arborea* and *angustata* show that the average genetic distance between *globosa* and these varieties is larger than that between those two varieties. The average pairwise F_{ST} value among *globosa* populations sampled is substantially less than that among *arborea* and *angustata* populations. Lewontin and Krakauer (1973) have argued that such a pattern might be expected if an entire section of a species complex originated from a relatively small isolated population that subsequently spread locally. We conclude, therefore, that Gitten's (1965) proposal that the ancestor of *globosa* was isolated from the other varieties and the globose form subsequently became fixed in this area is supported. Furthermore, the substantial genetic divergence detected between *globosa* and the other varieties as well as its clear morphological delineation leads us to the conclusion that *globosa* may deserve taxonomic placement as a subspecies of *Isomeris*.

Our results indicate that *I. arborea* is a species with moderate levels of genetic variation. For plant species exhibiting similar life-history characteristics (dicot, woody long-lived perennial, narrow geographic range, temperate distribution, outcrossing animal pollinated breeding system, early successional status) composite mean values from Hamrick and Godt (1990) for P , A , and H_E were 33.5%, 1.51, and 0.110 respectively. Corresponding values for *I. arborea* are substantially lower at 13.85%, 1.18 and 0.051. The gene diversity values we found in *I. arborea* are substantially different from that reported for similar species by Hamrick and Godt (1990, 1996): $H_T = 0.276$ vs. 0.320, $H_S = 0.152$ vs. 0.240, $G_{ST} = 0.449$ vs. 0.220 and $D_{ST} = 0.124$ vs. 0.07. The values we detected in *I. arborea* are, however, similar to those reported by Vanderpool et al. (1991) for the capers *Oxystylis lutea* and *Wislezienia refracta*. In addition to reporting a large number of unique alleles as found in this study, the apportionment of diversity among the populations they studied is quite similar to that reported here, ranging from 33 % for *Wislezienia refracta refracta* to 54 % for *Wislezienia refracta californica*. Furthermore, the average genetic diversity measures ($P = 23\%$, $A = 1.29$, $H_O = 0.075$ and $H_E = 0.073$) reported are more congruent to those we report.

Whether the patchy distribution of *I. arborea* observed today is a remnant of a more continuous range in the past is difficult to assess since no information on *Isomeris* exists in the fossil record (Iltis 1957; Iltis personal communication). The significant degree of structure among varieties is indicative of considerable isolation. Metapopulation cohesiveness within a landscape depends upon dispersal. If the interaction between the dynamics of dispersal and disturbance (climatic/geologic change) reaches some critical level, populations within the matrix may become disconnected and processes within them unpredictable. The repeated contraction and expansion of habitat associated

with the dynamic geologic and climatic history of the American Southwest may have played a major role in the distribution of genetic variation in *I. arborea*.

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VTM PLOTS AS EVIDENCE OF HISTORICAL CHANGE: GOLDMINE OR LANDMINE?

JON E. KEELEY

U.S. Geological Survey, Western Ecological Research Center, Sequoia National
Park, Three Rivers Canyon National Park, Three Rivers, CA 93271

jon.Keeley@usgs.gov

and

Department of Ecology and Evolutionary Biology
University of California, Los Angeles, CA 90095

ABSTRACT

VTM (Vegetation Type Map) plots comprise a huge data set on vegetation composition for many parts of California collected mostly between 1929 and 1935. Historical changes in vegetation have been inferred by sampling these areas many decades later and evaluating the changes in plant dominance. VTM plots can not be precisely relocated, and it has been assumed that errors resulting from this problem are inconsequential or can be eliminated by comparison with a composite of multiple contemporary plots. This study examines that assumption for southern California shrubland landscapes by comparing the differences in species composition between closely positioned VTM-sized plots. Comparing shrub species density in 400-m² plots separated by 30 m (center to center), I found that all species exhibited considerable differences in density even over this short distance. This patchiness in shrub distribution could lead to major errors in historical reconstructions from VTM plot data. Two methods are proposed for dealing with this problem. One is to collect multiple samples from the vicinity of the VTM plot and use the observed spatial variation to set bounds on the temporal changes required to represent significant historical change. The other is to look at broad landscape changes reflected in the averages observed in a large sampling of sites.

Key Words: chaparral, maps, photographs, plots, sage scrub, sampling.

Reconstructing historical changes in landscapes is becoming increasingly important as a means of understanding future climate change impacts. Techniques such as dendrochronology have been successfully applied to reconstructions of fire history and climate influences on tree growth but are of limited value outside of forests (Swetnam 1993; Skinner 1997). Phytoliths have proven success in recognizing changes in a variety of herbaceous and woody vegetation types (Bartolome et al. 1986; Delhon et al. 2003). Historical photographs have value in detecting broad landscape changes, but it is difficult to quantify the changes in vegetation composition (Gibbens and Heady 1964). Older sample plots are an increasingly valuable resource (Stephens and Elliott-Fisk 1998), and one database with great potential is the quantitative sample plots recorded by the Vegetation Type Map (VTM) project in California initiated in the early part of the 20th century (Wieslander 1935a).

The VTM project, under the direction of A. E. Wieslander mapped over 15 million hectares, or approximately 40 percent of the vegetation in California between 1929 and 1935 (Critchfield 1971). VTM maps were accompanied by quantitative sampling of more than 18,000 plots of 400-m² (800 m² in forests), field notes, and landscape photographs (Wieslander et al. 1933). These maps and associated data laid the foundation for our current understanding of plant community distribution in Cali-

fornia (Colwell 1977). Plot data, however, have perhaps received the most use and have contributed significantly to longstanding efforts at plant community classification within the state (Jensen 1947; Griffin and Critchfield 1972; Allen et al. 1991; Allen-Diaz and Holzman 1991) and to validate models of plant distribution (Vayssières et al. 2000; Franklin 2002).

Studies using VTM data for classification have implicitly or even explicitly assumed that there has been no significant change in vegetation over this time that would affect classification schemes. However, increasingly these VTM plot data are more important as historical records, and in recent decades all three of the VTM data types, maps, photographs and plot samples, have been utilized to reconstruct vegetation change.

Apparently the first use of these data for historical study was a comparison of both VTM plot data and accompanying photographic record with 1972 patterns in northeastern San Diego County (Bradbury 1974). The general conclusion from this study was that there had been relatively little change over this 41 year period, illustrated by a distinct landscape mosaic of chaparral and sage scrub along the Banner Grade Road in eastern San Diego County (Bradbury 1978).

Dodge (1975) also used VTM photographs to study historical changes in San Diego County vegetation. However, he found that most photographs

were close ups of vegetation types, and it was not possible to relocate the exact location for most of the ones he used in his study. He compared vegetation changes evident from re-photographing the same general area and concluded that 40 years of fire suppression had caused profound changes in vegetation. Taylor (2000) likewise presented pairs of VTM photographs and "retakes." He used written reference points to more precisely relocate sites (Alan Taylor, 9 July 2003 e-mail), and the similar tree spacing evident in the photos further suggests the paired photos were from the same site. Three of the four sites he presented were interpreted as providing evidence that decades of fire suppression contributed to increased forest density.

The original Wieslander maps also have been used to document historical changes. Freudenberger et al. (1987) quantified the grassland patterns recorded by the VTM maps and compared them with more recent vegetation maps for portions of Los Angeles and Ventura counties. Contrary to Bradbury's (1978) demonstration of stability in landscape patterns, they found very marked shifts in the distribution of grasslands and coastal sage scrub, which were tied to disturbance patterns.

While all three types of VTM data have been used for historical reconstructions, the plot data have received the greatest attention for reconstructions of vegetation change. These studies have been done in southern California shrublands (Bradbury 1974; Minnich and Dezzani 1998), central California oak woodlands (Holzman and Allen-Diaz 1991; Holzman 1993), and coniferous forests in the San Bernardino Mountains of southern California (Minnich 1978; Minnich et al. 1995) and the Sierra Nevada (Bouldin 1999). By contrasting contemporary plot samples with the VTM plot data, many of these studies have reported substantial changes in vegetation type and community composition. However, the precise location of VTM plots was never recorded so that it is not possible to actually "*resample*" the original 400 or 800 m² plots but only sample plots in the approximate vicinity of the original plots. Historical reconstructions from most of all of these studies presume that differences between the original VTM plot species composition and contemporary samples reflect temporal changes in these landscapes, but failure to adequately evaluate small scale spatial variation may lead to spurious conclusions about historical changes.

Since VTM plots cannot be precisely relocated and re-sampled, it is important to examine the scale of spatial variation on these landscapes. None of the VTM plot studies have evaluated the extent of spatial variation in the context of the estimated proximity of original and contemporary plots. A misplaced contemporary plot, or even a composite of plots, could be a poor baseline for examining historical changes with VTM data. The purpose of the present study was to evaluate assumptions behind studies that rely upon VTM plots as a baseline

for historical changes, and to evaluate limitations in the use of such data. Specifically, most VTM studies have implicitly assumed that imprecise alignment of plots does not interfere with conclusions about historical change. This study evaluates the extent of spatial variation in VTM-size plots that are separated by only 10 m in coastal sage scrub and chaparral communities in southern California. While these data do not specifically address the accuracy of VTM plot reconstructions for forest or woodland vegetation, they do reflect on assumptions used in those studies.

VTM PLOT HISTORY AND RECONSTRUCTIONS

One of the important drivers of the Vegetation Type Map project was concern with fire hazard in southern California chaparral (Colwell 1977), and thus this region had the most extensive and detailed coverage (Critchfield 1972). Sample plots were chosen to provide a fairly even geographic distribution of each vegetation type (outside of desert and alpine habitats) and age class. The sample protocol was designed to collect information for many purposes, including "unforeseen developments of the future" (Wieslander 1935b). The sample plots were rectangular ~400-m² plots (0.1 acre) or ~800-m² in forests with a length:width ratio of 4 (2 in forests) oriented perpendicular to the contour (Wieslander et al. 1933). Plots were laid out parallel to the ground surface and thus not slope-corrected, although this would not have made any detectable difference since plot boundaries were only visually estimated from a line running down the center of the plot.

Crews sampled non-forested plots by subdividing them into 100 equal size ~milacre squares, ~4 m² each. Only the dominant species in each square was recorded and it was assumed to fill the entire plot, thus representing 1% of the total plot cover. Where total cover was less than 50% the square was classified as bare ground. Data were expressed as frequency of squares dominated by each species. This metric represented relative cover and not ground surface cover, e.g., 100% cover only means shrub cover in each square was >50% and thus the plot could have had substantial bare ground. Because subordinate plants were not recorded from the squares, this methodology is inappropriate for estimates of density, and is of limited value for separating subsequent growth of subordinates from colonization and recruitment of new individuals. Height was also recorded and dead individuals indicated as such and squares lacking a dominant shrub or tree were recorded as bare ground, annual plants, cactus or *Pteridium*. A list of additional woody species was also recorded for each plot. In forest and woodland plots actual tree density was recorded for those individuals with a dbh over 10 cm, tallied in classes of ~10–30, 30–60, 60–90, and >90 cm, which were estimated, not measured (Bouldin 1999).

Plot locations were crudely indicated on a 1:62,500 topographic map by a hand-drawn circle with a radius ranging from approximately 110 m (Robert S. Taylor, Santa Monica Mountains National Recreation Area, 23 May 2003 email) to 300 m (Franklin 2002), describing an area of roughly 3.8 to 28 ha, respectively. In addition, the 19th century maps that were used were not accurate topographic maps that had been planimetrically surveyed, and thus contained substantial random and systematic errors (Bouldin 1999). Field notes included information on slope exposure (N, NW, W etc) and slope inclination, but these were based on visual estimates (according to former crew member Daniel Axelrod, personal communication cited in Bouldin 1999). Also of value in locating plots were notes on roads, rivers, prominent trees, and other prominent features, and this would contribute to more precise relocations in woodlands with older "landmark" trees. In addition to locational data, assessments were made of vegetation penetrability (i.e., ease of entering brush vegetation), parent rock material, evidence of erosion, and any special fire hazards due to snags. Countless other types of natural history data were collected, and voucher specimens added new species to our flora (e.g., Wieslander and Schreiber 1939).

Studies of historical changes in vegetation by "re-sampling" VTM plots have treated the problem of relocating the original plots differently. The only apparent criterion of Bradbury (1974, p. 29) was that the plots be relocated to "my satisfaction." On the other hand, Minnich (1978, p. 156) stated, "Unfortunately, they could not be precisely relocated from the mapped locations given on the VTM topographic sheets," and consequently, he used these data only as a means of providing the context for interpreting historical aerial photographs of coniferous forests.

In contrast, studies in central California oak woodlands by Allen-Diaz and Holzman (1991) and Holzman (1993) reported that by utilizing data taken by the VTM crews on elevation, slope aspect, and inclination, they could narrow the location of the re-sampling plot to within 5 m of the original plot center most of the time, and never more than 50 m. However, no information was presented on the types of evidence used to draw conclusions about this level of precision in relocating VTM plots. It was implicitly assumed in these studies that the level of spatial variation on these sites was insufficient to introduce significant error due to misplacement of the contemporary plots, but no supporting evidence was presented to substantiate this assumption.

Minnich et al. (1995) studied coniferous forests and reported with confidence that they could relocate, within 100 m, the original VTM plots, however, no details were given on how one might repeat this level of precision in relocating plots. They utilized field notes on distance to roads and prom-

inent trees, but did not explain how the figure of 100 m was derived or present evidence that this was based on anything more than "expert opinion." However, these investigators did acknowledge the likelihood that variation resulting from not placing the contemporary sample in precise alignment with the VTM sample could lead to erroneous conclusions about temporal variation. Their solution was to sample three plots within 0.5 ha of the presumed site of the VTM plot. They subjectively placed these three plots but gave no criteria for choosing the sample locations. This subjective placement of plots represents a major interpretation problem since their clearly articulated goal was to demonstrate historical changes due to fire suppression. These three plots were combined and averaged to produce a composite contemporary sample that could be compared with the historical data. This approach implicitly assumes that the mean of the current spatial variation in forest composition would produce a better basis for comparison with historical VTM plots than some other measure such as the variance in contemporary forest structure.

Minnich and Dezzani (1998) extended the use of VTM plots in an investigation of historical changes in the composition of sage scrub communities of western Riverside County. Despite the fact that they studied a very different community, and were attempting to relocate plots only half the size of those used in Minnich et al. (1995), they too reported they were able to relocate the original plots to within 100 m, but provided no protocol for repeating this level of precision. These authors also explicitly recognized that some change observed between the VTM plots and the contemporary samples could "be due to sampling error in relocation." To correct for this source of error, they sampled three plots subjectively scattered over an area of 1 ha; however, they did not explain why the sample area for this study was doubled over the 0.5 ha used in Minnich et al. (1995).

A different approach was followed in the extensive study of historical changes in northern Sierra Nevada conifer forests by Bouldin (1999). He acknowledged at the outset the inherent problems of precisely relocating VTM plots—"it proved infeasible in the Sierra Nevada because of the lack of on-the-ground markers and inaccuracies in original mapped plot locations." Consequently, Bouldin made no claims of being able to relocate VTM plots, rather he averaged the results from 2442 VTM plots sampled in 1935 and compared the patterns with 6221 contemporary USFS Forest Inventory and Analysis (FIA) plots distributed across the same region and sampled in 1992.

METHODS

To examine levels of spatial variation in southern California shrublands, I utilized data from an earlier study that included 90 sites of sage scrub or chap-

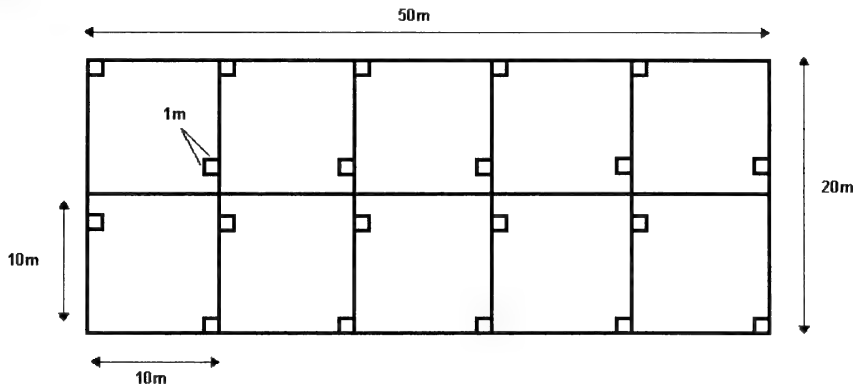


FIG. 1. Tenth-ha nested sampling method used in Keeley (1998) and Keeley and Fotheringham (2003). Plot is laid out with the long axis parallel to the contour. For this comparison the total density of shrubs in the two upper and two lower contiguous 100-m² subplots at the left end comprised a 400-m² plot and this was compared with a similar matching plot from the other end. Outer boundaries were separated by 10 m and by 30 m center to center. The 1-m² nested quadrats were not sampled for this study.

arral distributed over several counties (Keeley 1998; Keeley and Fotheringham 2003). Although these sites had burned prior to study, data utilized here comprised prefire shrub density estimates. Sampling used 1000 m² rectangular (20 × 50 m) sites subdivided into ten 100 m² subplots (Fig. 1). Within each site, two VTM size 400-m² plots could be assembled by combining four subplots at one end of the site and four at the opposite end. Thus, we have samples of prefire shrub density in matched VTM-size plots separated by 10 m. Since studies that have used VTM plots for historical reconstructions have stated that their re-samples were within 100 m of the original plot, our analysis of differences 30 m apart (center to center) should provide a lower limit of similarity to be expected in VTM studies in these vegetation types.

These plots were not identical to VTM plots because they were square and not rectangular, however, in these vegetation types, plot shape at this scale has no significant effect on species richness, cover, or density (Keeley and Fotheringham, in review). Another difference between the VTM sampling and this study is the metric used for comparison. Absolute shrub density is used here, rather than the relative measure of dominance used in the VTM sampling, a metric not clearly equated with either absolute cover or density. However, there is no reason to believe that the magnitude of spatial variation should be different between these two metrics. This conclusion is based on the fact that, regardless of density, the VTM plots only recorded a single individual from each milacre square, and in this study the mean density recorded for each species was less than one plant per milacre.

In this analysis the number of shrubs of each species were tallied for the 400-m² plot at one end of each of the 90 tenth-ha sites and compared with the number recorded from the plot at the other end of the site. For each species at each site, the dif-

ference in density between the two matched samples was expressed as a percentage of the mean calculated for the two samples.

RESULTS

Table 1 shows a comparison of shrub density for 18 species in matched 400-m² plots separated by 10 m (30 m center to center). Only species reported from more than a dozen sites were included in this table, and the focus was on the differences observed between these two “matched” plots. The smallest average difference observed was 67% for *Ceanothus megacarpus*, and most species exhibited >100% difference between plots.

In terms of absolute density, the difference between matched plots typically was on the order of 20–40 individuals, but for half of the species there was at least one site where the difference was hundreds of individuals (Table 1).

For nearly every species, these differences diminished greatly when all sites were combined; in other words when the left-side plots from all sites were summed, and that total compared with the total from all right-side matched plots, the differences were lower (Table 1). Thus, the differences between matched plots “averaged out” over large samples. This was affected by the number of sites a species occurred at, as illustrated in the negative relationship between sample size and difference calculated on the totals from all sites (Fig. 2).

DISCUSSION

The spatial variation observed in southern California shrublands suggests that species are clumped at a scale of 400-m² or less. As a consequence there is potentially a very significant error introduced if VTM plots are not precisely relocated or at least closer than the 10 m that separated paired plots in this study. Minnich et al. (1995) have made a valu-

TABLE 1. DIFFERENCE IN DENSITY BETWEEN MATCHED 400-m² PLOTS SEPARATED BY 10 m IN CHAPARRAL AND SAGE SCRUB VEGETATION, EXPRESSED AS 1) A PERCENTAGE OF THE MEAN BETWEEN THE MATCHED SAMPLES, 2) THE DIFFERENCE WHEN PLOTS FROM ALL SITES ARE FIRST COMBINED BEFORE CALCULATING THE DIFFERENCE, OR 3) THE ABSOLUTE DIFFERENCE IN DENSITY.

| Species | Number of sites | Average difference between matched plots (% of mean) $\bar{x} \pm \text{SE}$ | Difference when all matched plots from one end of the plot are summed and compared with the sum of those from the other end (% of mean) | Absolute difference | |
|--------------------------------|-----------------|---|---|---------------------|-------------------|
| | | | | Maximum | Mean of all sites |
| <i>Adenostoma fasciculatum</i> | 44 | 78 + 10 | 12 | 141 | 34 |
| <i>Artemisia californica</i> | 47 | 74 + 10 | 13 | 75 | 15 |
| <i>Ceanothus crassifolius</i> | 12 | 112 + 24 | 16 | 94 | 18 |
| <i>Ceanothus megacarpus</i> | 14 | 67 + 16 | 25 | 403 | 59 |
| <i>Cercocarpus betuloides</i> | 13 | 195 + 4 | 115 | 114 | 20 |
| <i>Encelia californica</i> | 13 | 123 + 20 | <1 | 283 | 82 |
| <i>Eriogonum fasciculatum</i> | 53 | 86 + 10 | 2 | 103 | 21 |
| <i>Hazardia squarrosus</i> | 33 | 125 + 13 | 8 | 476 | 41 |
| <i>Heteromeles arbutifolia</i> | 19 | 156 + 17 | 36 | 13 | 4 |
| <i>Malosma laurina</i> | 40 | 124 + 12 | 24 | 211 | 14 |
| <i>Mimulus aurantiacus</i> | 23 | 115 + 15 | 36 | 364 | 35 |
| <i>Quercus berberidifolia</i> | 20 | 105 + 18 | 3 | 32 | 5 |
| <i>Rhamnus crocea</i> | 52 | 137 + 10 | 8 | 56 | 4 |
| <i>Rhus integrifolia</i> | 20 | 100 + 15 | 35 | 74 | 14 |
| <i>Rhus ovata</i> | 15 | 145 + 17 | 51 | 5 | 2 |
| <i>Salvia apiana</i> | 18 | 104 + 14 | 7 | 86 | 19 |
| <i>Salvia mellifera</i> | 46 | 113 + 10 | 24 | 136 | 25 |
| <i>Yucca whipplei</i> | 29 | 120 + 13 | 5 | 29 | 7 |

able contribution by recognizing the potential for spatial variation confounding historical reconstructions when exact plot placement is impossible. Although the approach of sampling multiple plots and averaging those results to produce a composite

contemporary sample may seem intuitive (Minnich et al. 1995; Minnich and Dezzani 1998), there is no clear theoretical basis for this approach. While we have not compared the pattern of variation with three samples, the data in Table 1 illustrates that if two sample plots (10 m apart) are combined and averaged, the difference between the average and any one of the two plots may be rather large. When vegetation is patchy as in the case of these shrublands, a composite could be more dissimilar from the original VTM plot than any one of the individual sample plots.

I suggest that a more justifiable use of multiple contemporary samples is to calculate the level of spatial variance observed between these plots and use this as a baseline for interpreting the extent of real historical change. In other words, if the observed spatial variation exceeds the difference between the VTM plot and the contemporary composite samples, then there would be little justification for concluding that one is observing historical changes. Other methods for sorting out spatial effects on estimates of temporal change have been proposed (Stewart-Oaten et al. 1995; Benedetti-Cecchi 2003).

Based on the results from the present study, it seems likely that considering only those comparisons where the contemporary spatial variance is less than the difference between VTM and contemporary plots will ultimately lead to the exclusion of a substantial number of VTM—contemporary plot

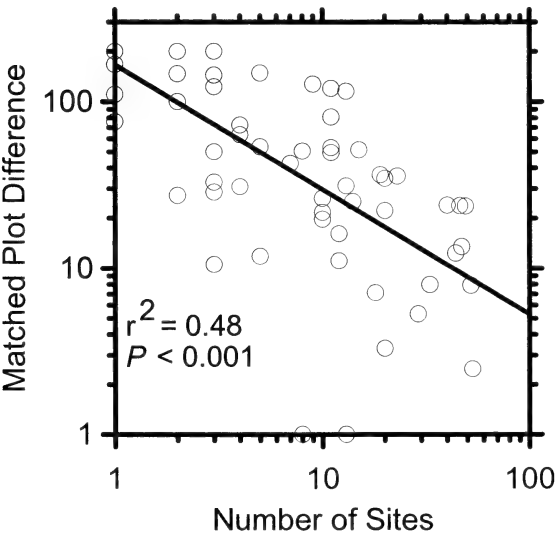


FIG. 2. Relationship number of sites occupied by a species and the difference between left-side plots vs right-side matched plots when calculated from the totals across all sites (column 3 from Table 1, also includes less common species not listed in Table 1).

comparisons. Thus, a preferable approach would be that pioneered by Bouldin (1999). He made no attempt to relocate VTM plots, rather he used the averages calculated from very large sample sizes and compared these with averages calculated on a large number of contemporary samples. Our data support that approach since differences between plots clearly even-out as sample size increases (Fig. 2). However, this is almost certainly a function of species density and similarity of sites under study, and these parameters would need to be determined for each study.

The results of the present study suggest that the broad generalizations about historical changes using VTM plots are likely valid; however, they raise serious questions about many of the very specific changes that are often based on single or just a few plots. For example, the reasonably large sample size ($n = 78$) of Minnich and Dezzani (1998) were likely sufficient to balance out any differences due to failing to precisely relocate contemporary sample plots. Thus, their generalization that sage scrub cover has declined during the 20th century is justifiable. However, many of the specific conclusions about changes in cover of particular species in Minnich (1978) and Minnich and Dezzani (1998) involved relatively small sample sizes, which are more likely affected by sampling error due to relocation problems. In addition, any species-specific comparisons of changes in cover are highly problematical because of the VTM protocol that only considers the cover of the dominant plant in each 4-m² square. It is easily possible for the cover of a species to remain the same from the time of the VTM survey to the present and yet be recorded as exhibiting dramatic declines in cover, if another species in many of the squares increased its cover during that period.

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A NEW SPECIES OF *MENTZELIA* SECTION *BARTONIA* (LOASACEAE)
FROM THE GREAT BASIN DESERT OF CALIFORNIA AND NEVADA

HENRY J. THOMPSON¹ AND BARRY A. PRIGGE²

Herbarium, University of California, Los Angeles, CA 90095-1606

ABSTRACT

A new species, *Mentzelia inyoensis* H.J. Thoms. & Prigge from Inyo and Mono counties, California and Churchill and Esmeralda counties, Nevada is described and illustrated. Based on chromosome number and floral and seed morphology, we consider *M. inyoensis* to be closely related to a group of species that include *M. candelariae*, *M. oreophila*, *M. leucophylla*, and possibly *M. pumila*.

Key Words: *Mentzelia*, *Mentzelia inyoensis*, Loasaceae, Great Basin.

Several collections of *Mentzelia* from Inyo and Mono counties, California and Esmeralda and Churchill counties, Nevada have been noted as being distinct but have never been formally described. Some of these collections passed as *M. multiflora* until H. J. Thompson and Joyce Zavortink realized that they were a new species. The earliest collection of this undescribed species was by K. Brandegee in 1913, reportedly from the east slope of the Sierra Nevada. This collection site has never been relocated. Then in 1949, P. A. Munz (Munz 13565, RSA) collected the new species in Silver Canyon, White Mountains, Inyo County.

The name was used as a *nomen nudum* in the *Jepson Manual* (Prigge 1993), and this publication legitimizes the name.

Mentzelia inyoensis H.J. Thoms. & Prigge, sp. nov. (Fig. 1). TYPE: USA, California, Inyo County, White Mountains, Silver Canyon, in wash at about 1935 m (6350 ft), 5 June 1968, J. Zavortink 3163 (chromosome voucher; Holotype: RSA; Isotypes: LA, MO, and NY).

Mentzelia candelariae similis sed petiolis longioribus (11–18 mm vice 6–10 mm) et stylis longioribus (10–13 mm vice 5–7 mm) et capsulis longioribus (12–25 mm vice 8–15 mm) et seminibus plus minusve parvis (2–3 mm vice 2.5–3.5 mm) atque papillis paucioribus per cellulas testae (2–6 vice 9–15) differt.

Erect perennials to 40 cm tall, densely vested with straight, retrorsely barbed hairs, the barbs in whorls of 3–6 including terminal whorl; stems several, from near the base, white. Rosette leaves lanceolate or oblanceolate, 4–11 cm long, 6–20 mm wide, crenate or irregularly and bluntly lobed, petiolate; cauline leaves lanceolate to linear-lanceolate, 6–10 cm long, 4–16 mm wide, sessile on lower stem and grading to clasping toward inflorescence; margins lobed; lobes blunt on lower leaves, narrow-

er and pointed on upper leaves. Flowers axillary or terminal, subtended by a bract; bract linear, entire or with a pair of short basal lobes or teeth; calyx lobes narrowly triangular, acuminate, 4.5–12 mm long, 1.3–3.2 mm wide; petals 5, yellow, elliptic to oblanceolate, 11–18 mm long, 2.2–4.0 (–6) mm wide, acute; petaloid staminodia 0; stamens numerous, 5–15 mm long, diminishing in length in inner whorls; anthers 0.6–1.4 mm long; filaments of the outermost whorls to 1.5 mm wide, becoming narrower in inner stamen whorls; style 10–13 mm long. Capsules straight, cylindrical, 12–16 (–25) mm long, 6–8 mm wide. Seeds lenticular, 2.0–3.0 mm long, 1.6–2.2 mm wide, narrowly winged, uniformly tannish or faintly tessellate; seed coat cells with straight radial wall and 2–6 papillae (Fig. 2), $n = 11$.

Mentzelia inyoensis has been collected from several substrates and habitats (carbonate rocks and gravel of scree slopes, washes, and canyon bottoms; calcareous pumice sand, whitish ash deposits, and clayey hillsides) and from sagebrush scrub, shadscale scrub, and pinyon-juniper woodland vegetation.

PARATYPES: USA, California, Inyo Co: White Mountains, Silver Canyon, 1981 m (6500 ft), P.A. Munz 13565 (RSA!); Silver Canyon, in wash at about 1953 m (6350 ft), J. Zavortink 3464 (LA!); Sierra Nevada(?), Andrew's Camp, near Bishop, K. Brandegee s.n. (RSA!, UC). Mono Co: White Mountains, 1.2 mi. N, 40°E of Red Mountain, Fishlake Valley drainage, 1661 m (5450 ft), T4S R35E S3, J.D. Morefield 3061 (NY, RSA!). Nevada. Churchill Co: 0.4 air miles SSE of junction of hwy 50 and 2, T17N, R36E, sec. 31, 1463 m (4800 ft), A. Tiehm, P. Lott, and J. McCormick 5824 (LA!, NY), A. Tiehm and B. Prigge 10764 (chromosome voucher; LA!), B. Prigge and A. Tiehm 7308 (LA!). Esmeralda Co: White Mts., Busher Creek Campground, 1.5 mi NE 25° of Juniper Mt. summit, T3S R35E S7, 1707 m (5600 ft), J.D. Morefield 4005 (LA!, NY, RSA!).

As an aid to the identification of *Mentzelia* (section *Bartonia*) from the Intermountain Region of

¹ Retired.

² Author for correspondence, email: bprigge@ucla.edu

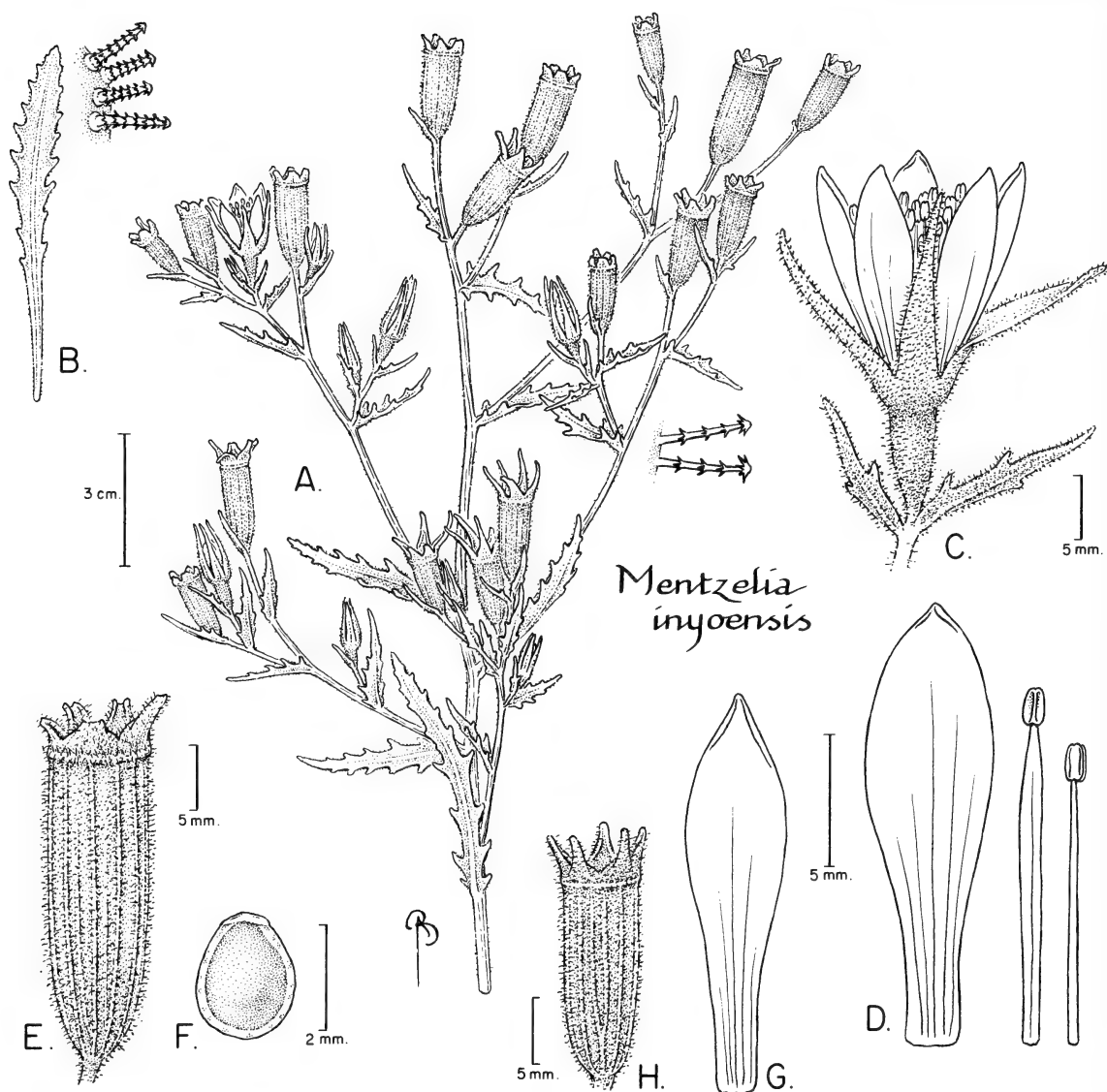


FIG. 1. *Mentzelia inyoensis*. A) portion of mature plant with buds, flowers, and fruits and detail of barbed hairs from stem; B) cauline leaf with detail of barbed pubescence; C) lateral view of partially opened flower; D) series showing petal, a stamen from outermost whorl, and a stamen from an inner whorl; E) fruiting capsule; F) seed with narrow wing; G) petal; and H) immature capsule.

California and Nevada, we present a species \times character matrix (Table 1) using mostly some diagnostic characters. The species in the table are ordered so that species with characters that match more closely with those of *M. inyoensis* are placed closer to that species. In ordering the species, we emphasized characters of the seed coat, especially the radial wall, chromosome number (ignoring the count for *M. leucophylla*, see footnote 5 in Table 1), petaloid staminodia, and petaloid stamens. The other characters in the table also contributed to species ordering but most of the ordering was accomplished by the emphasized characters.

Radial wall shape and surface papillation of seed coat cells have proven to be useful characters for defining and identifying many species of *Mentzelia* section *Bartonia* (Hill 1976; Thompson and Prigge 1984, 1986; Prigge 1986; Christy 1997; Holmgren and Holmgren 2002). However, these characters are perhaps less useful in the California and Nevada portions of the Intermountain Region because most of the species have straight radial walls and several species have poorly defined papillae or sometimes a covering layer that obscures the papillae, both of which makes counting the number of papillae difficult.

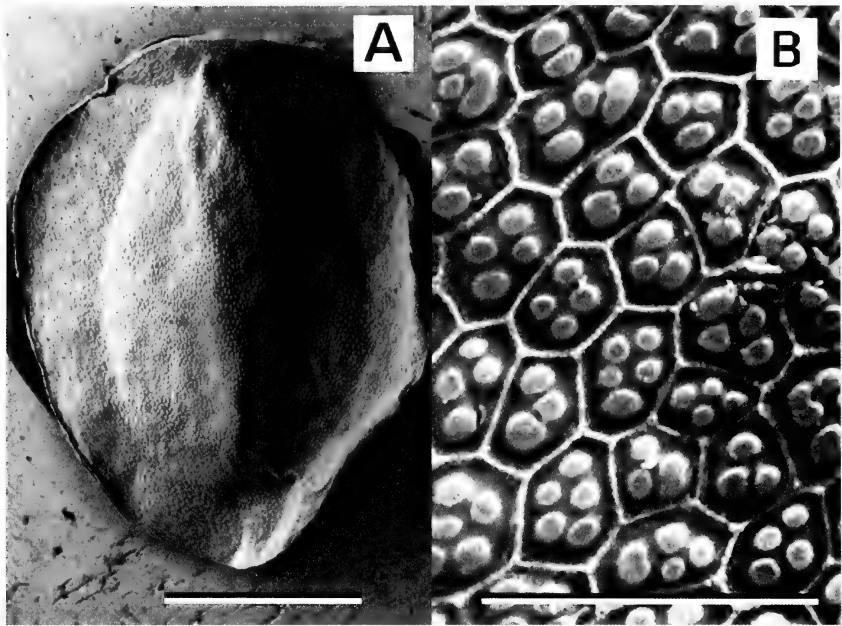


FIG. 2. Scanning electron micrographs of *Mentzelia inyoensis* seed: A) whole seed, hilum at top, bar = 1 mm; B) seed surface features showing straight radial walls of seed coat cells and 2–5, well defined papillae per cell, bar = 100 μ m. Seed is from Zavortink 3164 (collected from the type locality).

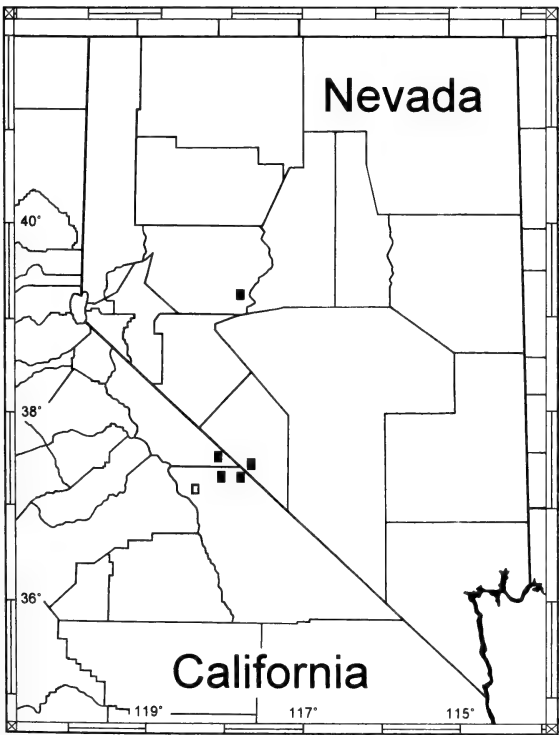


FIG. 3. Distribution of *Mentzelia inyoensis* (■). Brandegee's collection from Andrew's Camp in the Sierra Nevada (□), a location we regard as questionable, see text for further comments.

As shown in Table 1, *Mentzelia inyoensis* is very similar to *M. candellariae* and is part of a group of *Mentzelia* species that have a chromosome number of $n = 11$, a seed morphology where the seed coat cells have straight radial walls, the petals are glabrous except for a few hairs at apex (pubescent petals occur in *M. cronquistii* H.J. Thoms. & Prigge and *M. marginata* (Osterh.) H.J. Thoms. & Prigge of Utah and Colorado), and petaloid staminodia are absent. In Wyoming and northeastern Utah, another species that lacks petaloid stamens and has few papillae on the seed coat cells, commonly identified as *M. pumila* (Nutt.) Torr. & A. Gray, may prove to be more similar than *M. candellariae*. However, its seed morphology may not be typical of *M. pumila* and may be indicative of another undescribed species. More field work and a careful evaluation of the type material are necessary before this can be resolved.

Mentzelia inyoensis is believed to be restricted to the Reno and Tonopah floristic regions of the southwestern Great Basin (Holmgren, 1972) and is currently known from only five general localities (Fig. 3). A sixth collection by K. Brandegee in 1913 from Andrew's Camp near Bishop is an uncertain location. The only Andrew's Camp that we have found near Bishop is in the Sierra Nevada on Bishop Creek. Attempts by J. Zavortink and us to collect this species in the drainage of Bishop Creek were unsuccessful. According to Lloyd & Mitchell (1973), K. Brandegee also collected in Silver and Coldwater canyons in the White Mountains in

TABLE 1. MATRIX OF CHROMOSOME NUMBERS AND FLORAL, FRUIT, SEED, AND LEAF CHARACTERISTICS FOR SPECIES OF *MENTZELIA* SECTION *BARTONIA* FROM THE INTERMOUNTAIN FLORA OF CALIFORNIA AND NEVADA. Abbreviations: br. = broadly; nar. = narrowly, unk. = unknown. ¹ Chromosome counts are those reported on herbarium and annotation labels of specimens at LA (mostly counted by H.J. Thompson) and from Thompson (1963) unless noted otherwise. ² This term, following Brown and Kaul (1981) and Hufford (1989), refers to what appears to be an inner whorl of five petals but are sterile stamens with expanded filaments. ³ The outermost stamens with filaments that are greatly expanded and petal-like, i.e. the filament is as wide or nearly as wide as the petal, but bears a fertile anther. In dried material anthers are easily dislodged which can result in their appearance as petaloid staminodia. ⁴ Papillae are counted from the body of the seed; not the wings. ⁵ Reveal & Styer (1973). This count needs to be checked. We would expect a count that would fit with the aneuploid series that exists in section *Bartonia*. ⁶ From Holmgren and Holmgren (2002). ⁷ *Mentzelia laevicaulis* has an outer whorl of five distinctive stamens with an expanded filament ca 2 mm wide but not like the petals. ⁸ From Christy (1995 and 1998) and our records.

| Species | Chromosome number (n) ¹ | Petal length (mm) | Petaloid staminodia ² | Petaloid stamens ³ | Capsule | | |
|--|--|----------------------|-------------------------------------|----------------------------------|--|----------------|---------------|
| | | | | | Shape | Length (mm) | Width (mm) |
| <i>M. inyoensis</i> H.J. Thomps. & Prigge | 11 | 11–18 | 0 | no | cylindrical | 12–16 (–25) | 6–8 |
| <i>M. candalariae</i> H.J. Thomps. & Prigge | 11 | 6–10 | 0 | no | bowl-shaped to subcylindrical | 8–15 | 5–8 |
| <i>M. oreophila</i> J. Darl. | 11 | 7–14 (–17) | 0 | yes | br. bowl-shaped | 5.5–6.5 | 6–7.5 |
| <i>M. leucophylla</i> Brandegee <i>sensu</i> <i>stricto</i> | 18 ⁵ | 10–11 | 0 | yes | br. bowl-shaped | 5–10 | 7.5–8.2 |
| <i>M. tiehmi</i> N.H. Holmgren & P.K. Holmgren ⁶ | unk. | 7–15 | 0 | yes | bowl-shaped | 5–9 | 4–6 (–7) |
| <i>M. argillicola</i> N.H. Holmgren & P.K. Holmgren ⁶ | unk. | 8.5–15 | 0 | yes | deeply bowl- shaped | 5.5–10 | 4–5.5 |
| <i>M. polita</i> A. Nelson | 11 | 7–13 | 0 | yes | bowl- to short barrel-shaped | 5–10 | 6–9 |
| <i>M. pterosperma</i> Eastw. | 11 | 9–24 | 5 | yes | bowl- to barrel- shaped | 8–15 | 6–10 |
| <i>M. laevicaulis</i> (Doug. ex Hook.) Torr. & Gray | 11 | 40–80 | 0 | no ⁷ | cylindrical | 24–45 | 10 |
| <i>M. integra</i> (M.E. Jones) Tidestr. | 10 | 8–20 | 5 | yes | bowl-shaped to thick cylindri- cal | 8–18 | 5–10 |
| <i>M. multiflora</i> (Nutt.) Torr. & A. Gray ⁸ | 9 (10) | 9–25 | (0) 5 (10) | yes/no | cylindrical, barrel- or bowl-shaped | 10–20 | 5.5–8.5 |

1913, and we believe she may have collected *Mentzelia inyoensis* from one of these canyons (probably Silver Canyon). She also collected at McGee Meadows, Birch Creek, and Red Hill (west of Bishop) at the end of June or start of July, 1913 (see http://mip.berkeley.edu/www-apps/smasch/smasch_accession.html and search for Inyo County, Brandegee, and 1913) and one of these areas may also be where she collected *M. inyoensis*. Although we regard her specimens of *M. inyoensis* as mislabeled, someone may eventually find it in the vicinity of Bishop Creek or elsewhere in the Sierra Nevada and thereby confirm its occurrence in that mountain range.

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TABLE 1. EXTENDED.

| Seed | | | | Lower Cauline Leaf | | |
|----------------|-----------------------|-----------------|-----------------------------------|--------------------|--|---|
| Length (mm) | Wing width (mm) | Coat | | Length (cm) | | |
| | | Radial walls | Papillae per cell ⁴ | | Outline | Margins |
| 2.0–3.0 | 0.2–0.5 | straight | 2–6 | 6–10 | lanceolate to linear lanceolate | lobed |
| 2.5–3.5 | 0.3–0.6 | straight | 9–15 | 2–10 | linear lanceolate | irregularly dentate, shallowly lobed, entire |
| 2.7–2.9 | 0.4–0.9 | straight | 3–7 | <9 | elliptic to ovate | undulately toothed |
| 2.8–3.8 | 0.4–0.9 | straight | 6–15 | 2.4–10 | lanceolate to oblanceolate, ovate | br. and shallowly round toothed |
| 2.2–2.5 | 0.1–0.3 | straight | 15–40 | 1.5–5 | oblanceolate | weakly lobed to subentire |
| 2.0–2.4 | 0.1 (–0.2) | straight | 5–8 | 2–3.7 | nar. oblanceolate | undulate toothed or shallowly lobed |
| 2.5–3.0 | 0.5–0.8 | straight | 4–13 | <7 | nar. oblanceolate, linear, nar. lanceolate | gen entire (or with a small rounded tooth) |
| 3.0–4.0 | 0.8–1.1 | straight | 10–15 | <6 (9) | oblanceolate or obovate to br. lanceolate | crenate, toothed, or entire |
| 2.0–4.0 | 0.4–0.5 | straight | 3–5 | 5–15 | lanceolate to oblanceolate | lobed |
| 2.5–4.0 | 0.5 | wavy | 6–10 | <13 | nar. elliptic to lanceolate | entire or undulately toothed or shallowly lobed |
| 2.0–4.0 | 0.4–1.0 | sinuate | ∞ | <15 | nar. elliptic to lanceolate (oblanceolate) | toothed to lobed, sometimes pinnatifid |

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A NEW SPECIES OF *SILENE* (CARYOPHYLLACEAE) FROM THE
SERPENTINES OF DEL NORTE COUNTY, CALIFORNIA

THOMAS W. NELSON AND JANE P. NELSON
4244 Fairway Drive, Eureka, CA 95503-6413
janetomnel@humboldt1.com

ABSTRACT

Silene serpentinicola T. W. Nelson and J. P. Nelson is here described as new, discovered on and endemic to the serpentines of the Smith River basin, within Six Rivers National Forest, Del Norte County, California. The bright carmine-red flowered *S. serpentinicola* has been confused and with the red-scarlet flowered *S. californica* Durand and the pink of *Silene hookeri* Nutt subsp. *pulverulenta* (Peck) Hitchc. & Mag. However, each is distinctive.

Key Words: *Silene*, serpentine, Smith River Basin, Six Rivers National Forest, Del Norte County, California.

Silene serpentinicola T. W. Nelson and J. P. Nelson, sp. nov. (Fig. 1)

A *Silene californica* in caule uno e rhizomate ramificante enascens et caulis secundis interdum in iodem rhizomate brevioribus (4–10 nec 20–50 cm) floribus paucioribus (1–3 vel nec 2–5) floribus bicoloribus unguibus albis vividus puniceus sursum limbis vividis puniceis appendicibus (2.5–4.5 × 0.5–1 mm nec 1–1.5 × 0.5–0.75) truncates (nec fimbriatis) ad apicem divergens.

Perennial; stems from thin branching rhizome system attached to deep tap root, erect, 4–10 (15) cm long, simple, gray-green, canescent, eglandular at base, glandular-pubescent above; cauline leaves of 4–8 pairs, crowded, oblanceolate to obovate, the lowest reduced to lanceolate bracts upward increasing in size, 2.5–4.5 cm long, 0.5–1.5 cm. wide, gray-green, glabrate; inflorescence terminal, 1–3 (4) flowered, densely glandular pubescent; calyx purplish, inflated tubular expanding in fruit, indistinctly 10-nerved, densely glandular pubescent, 13–17 mm long; limb of corolla carmine-red, purple on drying, more or less equally 2-lobed, each lobe with a lateral tooth, claw white with increasing carmine-red veining distally, the limb considerably wider than claw; petaloid appendages 2, prominent, linear, truncated, 2.5–4.5 mm long, 0.5–1.0 mm wide; filaments 17–25 mm long, long exerted; styles 3, 13–17 mm long, long exerted; seeds reniform, dark brown, strongly papillate 1.8–3.0 mm long; hexaploid, $2n = 72$ (Kruckeberg 1960).

Type: USA, CA, Del Norte County, T18N, R1E, Sec. 34, UTMS N 4641021 E 413668, Elev. 589 m (1933 ft), Six Rivers National Forest, Low Divide road 8.85 miles north of junction with North Bank road. Serpentine road cut just South of Low Divide, 20 June 2002, *Thomas W. Nelson & Sydney Carothers* 9175. (HOLOTYPE: HSC; Isotypes: BYU, CAS, OSC, MICH, RM, RSA, UC, US, WTU.

Paratypes: USA, CA, Del Norte County: Flowers

bright red, gravely opens on Red Hill, 13 Jul. 1907, *W.L. Jepson* 2904 (JEPS); Near Gasquet, North side of Middle Fork of Smith River on Old Gasquet Toll Road, 1 Jun. 1935, *Harold E. Parks & Joseph P. Tracy* 11205 (UC); Low Divide East of Smith River Village in chaparral, serpentine, Elev. 549 m (1800 ft), 25 Jun. 1938, *Joseph P. Tracy* 16199 (UC); Humboldt Flat South of Adams Station, serpentine, Elev. 762 m (2500 ft), 26 Jun. 1952, *Philip Munz*, 17790 (RSA); T17N, R2E, Sec. 16, Jct. Stony Creek & North Fork Smith River, 23 May 1972, *Larry De Buhr & Garry Wallace* 617 (RSA); dry rocky bank along Low-High Divide Rd. 7.4 miles from junction with North Bank Road, 13 Jun. 1956, *E. K. Balls & L. W. Lenz*, 21673 (RSA); T17N, R1E, Sec. 25, along French Hill Rd. 0.6 miles from junction with State Route 199, moist serpentine, 14 Jun. 1978, *Thomas Nelson & Jane Nelson*, 4151 (HSC, RSA, WTU); Gasquet Quad, Elev. 419 m (1374 ft) near 18 Mile Creek, 15 Jun. 1988, *Dave Imper* 1422 (HSC); 4 miles south of state route 199 on South Fork Smith River Road, serpentine gravel bank, 27 Jun. 1984, *Dave Imper* s.n. (HSC); near High Divide, serpentine lat. 41°54'42" long. 124°02'55" 14 Jun. 1982, *Dave Imper* 1425 (HSC); T17N, R2E, Sec. 31, off French Hill Road in serpentine openings, 6 Jul. 1983, *Tom Jimerson* s.n. (HSC); along High-Low Divide Road 5.8 miles from junction with North Bank Road, dry serpentine, Elev. 518 m (1700 ft), UTMS N 04113739 E 463743, 18 Jun. 2002, *Thomas Nelson & Sydney Carothers* 9085 (HSC); T18N, R1E, Sec. 34, UTMS N 0413905 E 4640976, Elev. 488 m (1600 ft) along Low Divide Rd. ca. 0.75 miles south of Low Divide, serpentine on road cut, 13

FIG. 1. Illustration of *Silene serpentinicola*. A. Mature plant at anthesis and plant in bud. B. Petal showing appendages. C. Flower in longitudinal section.

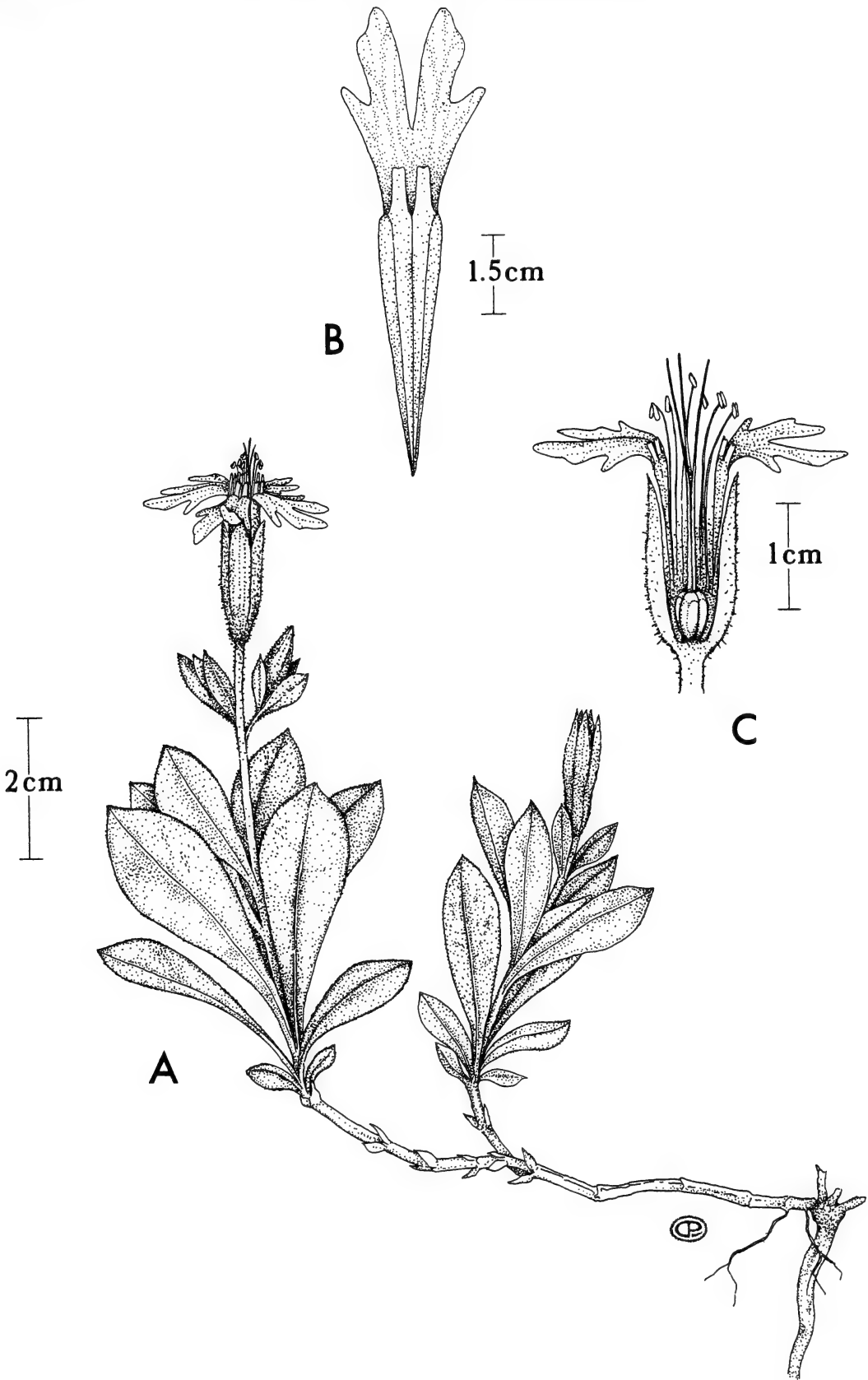


TABLE 1. COMPARISON OF DISTINGUISHING FEATURES OF *SILENE SERPENTINICOLA* WITH *SILENE CALIFORNICA* AND *SILENE HOOKERI* COMPLEX

| | <i>S. serpentinicola</i> | <i>S. californica</i> | <i>S. hookeri</i> complex |
|----------------------|---|--|--|
| Habit | One (two) erect stems from thin branching rhizome | Three to five reclining stems from root crown | Three to five reclining stems from root crown |
| Corolla limb | Carmine-red | Red-scarlet | Pink-white |
| Corolla claw | White with carmine-red veining above | Red-scarlet | Pink-white |
| Filaments and styles | Long exerted | Long exerted | Included |
| Pubescence | Densely glandular | Slightly glandular | Canescent |
| Petaloid appendages | Truncate 2.5–4.5 mm long × 0.5–1.0 mm wide, prominent | Fimbriate, 1.0–1.5 mm long × 0.5–0.75 mm wide, not prominent | Truncate, 0.8–1.3 mm long × 0.5–0.7 mm wide, not prominent |
| Habitat | Serpentine endemic | Occasionally found on serpentine | Mostly found on serpentine |

Jun 2002, *Thomas Nelson & Sydney Carothers*, 9089 (HSC); T17N, R2E, Sec. 29, along French Hill Rd. 2.4 miles from junction with State Route 199, serpentine, 14 Jun. 1978, *Thomas Nelson & Jane Nelson*, 4164 (HSC); T17N, R2E, Sec. 18, along Forest Service Rd. 305 (Gasquet Mountain Rd.) 2 miles from junction with State Route 199, serpentine, 15 Jun. 1989, *Thomas Nelson & Jane Nelson* 8753 (HSC); T17N, R1E, Sec. 9, Elev. 640 m (2100 ft), along Forest Service Rd. 305, 6 miles north of junction with North Bank Rd., serpentine, 24 May 1987, *Thomas Nelson & Jane Nelson*, 8981 (HSC); T17N, R2E, Sec. 20, Gasquet Rd. (Old Gasquet Toll Rd.), May 29 1947, *Ruby Van Deventer*, s.n., (HSC); T17N, R2E, Sec. 16, Elev. 183 m (600 ft), Stony Creek Bog, Jeffrey Pine & Incense Cedar, 13 May 1973, *James P. Smith*, 6718 (HSC); T17N, R2E, Sec. 21, Elev. 145 m (475 ft), Old Gasquet Toll Rd., disturbed chaparral under power lines 0.2 miles north of southern entrance, 17 Jun. 1976, *Linda Barker*, 1611 (HSC); along road side near meteorological tower, Little Bald Hills, T16N, R1E, Sec. 23. Elev. 549 m (1800 ft), 28 Jun. 1984, *Lois Reed*, s.n. (Redwood National Park Herbarium).

DISTRIBUTION AND HABITAT

Silene serpentinicola is a rare species endemic to serpentes of the Smith River Basin of northwestern Del Norte County, extreme northwestern California. Although we have found no populations in extreme southwestern Oregon, the serpentine sequences of Del Norte County extend into this area.

RELATIONSHIPS

Although *S. serpentinicola* has been confused with *S. californica* and *S. hookeri* subsp. *pulverulenta*, each of the three is distinctive. Table 1 details the important differences. Kruckeberg (1960) determined the chromosome numbers of the three *Silene* species in this paper to be: *S. serpentinicola* 2n = 72 (hexaploid), *S. californica* 2n = 48 (tetraploid), and *S. hookeri* 2n = 72 (hexaploid). Furthermore, artifical crosses between *S. serpentinicola* and *S. hookeri* demonstrated reduced fertility in the F-1 generation and marked infertility in the F-2 generation (Kruckeberg 1961). At least one population is known where the two species are sympatric and no intermediates are present.

ACKNOWLEDGMENTS

We wish to thank Dr. Stanley Welsh for the Latin and Ms. Christana Paleno for the illustration. We appreciate the hospitality and services of the staffs and loan of specimens from UC, JEPS and RSA herbaria. We especially thank Dr. James P. Smith, Jr. and Robin Bencie for access to the excellent collections at HSC. We also thank Lisa Hoover, Forest Botanist of Six Rivers National Forest, for her support and Sydney Carothers, botanist in the Six Rivers National Forest, for her assistance in the field and of her knowledge of the plants growing within the Six Rivers National Forest.

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**BOECHERA YORKII (BRASSICACEAE), A NARROW ENDEMIC FROM THE
LAST CHANCE RANGE, DEATH VALLEY NATIONAL PARK,
INYO COUNTY, CALIFORNIA**

STEVE BOYD

Herbarium, Rancho Santa Ana Botanic Garden, Claremont, CA 91711,
steve.boyd@cgu.edu

ABSTRACT

Boechera yorkii S. Boyd is described as a new species. It is a narrow endemic from the Last Chance Range in Death Valley National Park, Inyo County, California, apparently restricted to carbonate substrate. *Boechera yorkii* is distinguished from all other *Boechera* taxa in the Death Valley region by having reflexed flowers and yellow petals with brick-red tips (rarely all yellow or all brick-red) rather than all white, pinkish, purple, or some combination of these. Conservation concerns are limited as all currently known populations occur in a relatively inaccessible area, entirely within Death Valley National Park boundaries.

Key Words: *Boechera*, *Arabis*, Brassicaceae, carbonate, endemic, Last Chance Range, Death Valley.

Dana York, Death Valley National Park Botanist, encountered an unfamiliar Brassicaceae growing on carbonate substrate in the Last Chance Mountains, east of Eureka and Saline valleys during the spring of 2000. In leaf vestiture, overall floral morphology, and habit, the plants were well-placed within the genus *Boechera* Löve & Löve, but were noteworthy in having reflexed flowers with the petals yellow proximally becoming reddish at the tips, as opposed to the purplish, pinkish, or whitish petals found in other *Boechera* taxa known from the region. York collected a voucher specimen in flower and young fruit, and photographed the plants *in situ*. These were sent to me for examination. York provided additional flowering specimens collected in 2001, but was unable to find mature fruit due to extensive herbivory of plants within the population.

Comparing York's specimens to material in the herbarium of Rancho Santa Ana Botanic Garden (RSA-POM) and to descriptions in various floristic and monographic treatments, I was unable to ascribe these to any known *Boechera* taxon. A suite of vegetative and floral characters, in particular leaf vestiture, floral orientation, corolla symmetry, and petal color, readily distinguishes York's plants from other species of *Boechera*. Consequently, I propose here the recognition of a new species, *Boechera yorkii*.

Boechera yorkii S. Boyd, sp. nov. (Fig. 1).—Type: USA, California, Last Chance Range, on the N side of a canyon 440 m S of Last Chance Mountain; 37°16'35.9"N, 117°41'47.2"W (NAD 27); 2410 m (7910 feet); 16 May 2001, *Dana York & Kathy Davis 2611* (holotype RSA; isotypes CAS, MO). Paratype: USA, California, Last Chance Range, on the N side of a canyon 880 m SW of Last Chance Mountain; 37°16'24.9"N, 117°42'17.4"W (NAD 27), 2220 m (7280 feet); 16

May 2001, *Dana York & Kathy Davis 2616* (DEVA).

Differt a *B. dispar* (M.E. Jones) Al-Shehbaz et *B. inyoensis* (Rollins) Al-Shehbaz floribus reflexis corollis subzygomorphis petalis proximalium flavorum distalium lateritorum (vel totis flavorum vel totis lateritorum) ovariis pubescentibus dendriticis.

Perennial herb from \pm branched, woody caudex; stems erect, 10–30 cm long, unbranched or with small lateral branches at the uppermost cauline leaves, tomentum moderately dense with numerous short, dendritic trichomes and scattered longer, few-branched trichomes, especially below inflorescence; basal leaves gray-green, numerous, ascending, entire, linear-oblongate to spatulate, apex acute to \pm rounded, 0.5–4 cm long (including the broad petiole), 1.5–3 mm wide, leaf epidermis readily visible under tomentum of numerous loose dendritic trichomes and scattered longer, entire to few-branched hairs; cauline leaves gray-green, grading from linear-oblongate below to linear or narrowly lanceolate near the inflorescence, but not much reduced in length, auricles lacking or vestigial, vestiture similar to basal leaves, but dendritic trichomes less dense; inflorescence racemose, lowest 1–2(3) flowers often subtended by narrow linear bracts 4–6(10) mm long, \pm similar to cauline leaves or with narrow hyaline margin that lacks trichomes (i.e., \pm sepaloid), pedicels stout, short, reflexed, 1–1.5 mm at anthesis, with dense, short, dendritic trichomes; flowers \pm reflexed at anthesis; calyx cylindric, sepals linear-oblong, greenish, ca. 5 mm long, 1.2 mm wide, with moderately dense dendritic trichomes abaxially; corolla slightly zygomorphic due to petal orientation, petals erect, the tips and upper $\frac{1}{3}$ of blade spreading-recurved, linear, 9–10 mm long, ca. 0.8 mm wide, brick-red in distal $\frac{1}{3}$ grading to pale yellow (rarely yellow or

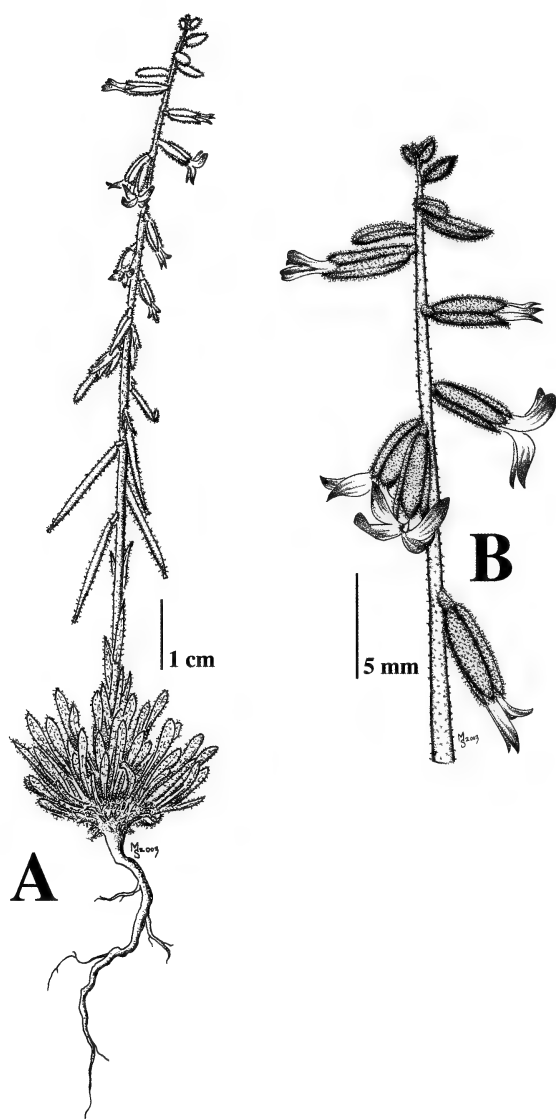


FIG. 1. *Boecheera yorkii*. A) general habit of a flowering rosette in early fruit. B) detail of upper inflorescence showing vestiture of stem and calyces, \pm deflexed orientation of flowers at full anthesis, and slight zygomorphy of corollas.

brick-red throughout), glabrous or with a few scattered dendritic trichomes on abaxial surface distally; *stamens* 6, tetradynamous, included, filaments pale yellow, \pm equal, ca. 4 mm long, anthers of longer stamens ca. 1.2 mm long, those of shorter stamens ca. 1.6 mm, pollen ellipsoid, tricolpate (Fig. 2); *ovary* linear, ca. 2.5 mm long at anthesis, densely covered with short, dendritic trichomes, style ca. 0.25 mm long, stigma \pm 2-lobed; *fruit* a narrowly linear capsule on reflexed pedicel (Fig. 3), moderately to sparsely pubescent with short dendritic trichomes, straight or very slightly arcuate (fully mature fruit and seeds unknown).

The specific epithet honors Dana York, Death Valley National Park Botanist, who discovered the plant. He suggests using "Last Chance rock cress" as the vernacular name for this rare species.

DISCUSSION

Recent molecular, morphological, and cytological studies have demonstrated the genus *Arabis*, as traditionally and broadly circumscribed (e.g., Rollins 1993), to be polyphyletic, representing an assemblage of four genera: *Arabidopsis*, *Boecheera*, *Pennellia*, and *Turritis*, in addition to *Arabis* s. str. (Al-Shehbaz 2003). In the New World, the majority of taxa traditionally treated as *Arabis* s.l. have a base chromosome number of $x = 7$, and comprise the genus *Boecheera* (Al-Shehbaz 2003). *Boecheera*, as presently circumscribed, is most diverse in western North America, especially within the Great Basin and Mojave deserts (Rollins 1941, 1993; Al-Shehbaz 2003).

At least 14 taxa of *Boecheera* are known from the Death Valley region of eastern Inyo County, California (Kurzius 1981; Norris 1982; Schramm 1982; DeDecker 1984; Annable 1985; Peterson 1986). The Death Valley region is interpreted here as including the Argus and Inyo mountain ranges, as well as the valleys and ranges adjacent to Death Valley, but excluding the White Mountains. This is an area transitional between the Great Basin and Mojave Desert floristic regions, and noted for supporting large number of endemic species and genera (Raven 1977). Other *Boecheera* taxa documented from the Death Valley region include *B. cobrensis* (M.E. Jones) Dorn, *B. dispar* (M.E. Jones) Al-Shehbaz, *B. glaucovalvula* (M.E. Jones) Al-Shehbaz, *B. holboellii* (Hornem.) A. Löve & D. Löve (incl. *Arabis holboellii* Hornem. var. *pendulocarpa* (A. Nelson) Rollins, *A. holboellii* var. *retrofracta* (Graham) Rydb.), *B. inyoensis* (Rollins) Al-Shehbaz, *B. lyallii* (S. Watson) Dorn (incl. *Arabis davidsonii* Greene var. *parva* Rollins), *B. microphylla* (Nutt.) Dorn var. *microphylla*, *B. perennans* (S. Watson) W.A. Webber, *B. pulchra* (M.E. Jones ex S. Watson) W.A. Webber var. *gracilis* (M.E. Jones) Dorn, *B. pulchra* var. *munciensis* (M.E. Jones) Dorn, *B. pulchra* var. *pulchra*, *B. shockleyi* (Munz) Dorn, and *B. sparsiflora* (Nutt.) Dorn var. *sparsiflora*.

In overall appearance, *Boecheera yorkii* is vegetatively similar to many *Boecheera* taxa from the arid mountains of western North America; i.e., generally caespitose, each rosette a dense cluster of spatulate to narrowly oblanceolate leaves appearing gray-green to ashy-white due to a tomentum of low, dendritic trichomes. Of those *Boecheera* taxa previously documented from the Death Valley region, *B. yorkii* is most similar vegetatively to *B. dispar* (leaf shape, overall habit, size of rosettes) and *B. inyoensis* (leaf shape, tomentum). It is readily separable from these two taxa by several floral and

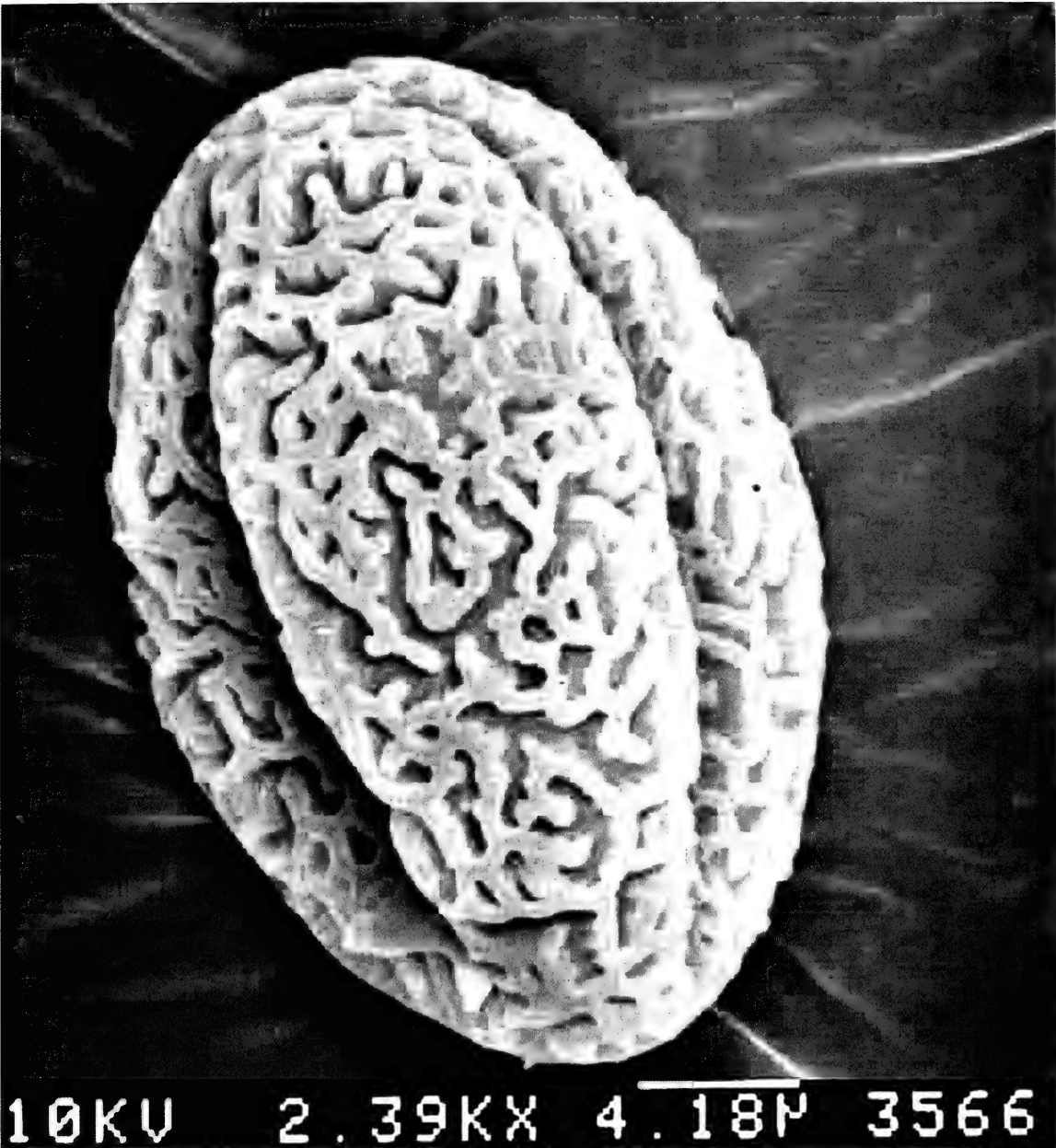


FIG. 2. Scanning electron micrograph (SEM) of ellipsoid, tricolpate pollen grain of *Boechera yorkii* [York & Davis 2611 (RSA)].

fruit characters, however. The most striking differences among these three taxa are found in the color, size, and shape of the petals, pedicel angle in fruit, and vestiture of the young fruit.

Boechera yorkii stands out among nearly all species of *Boechera*, including *B. dispar* and *B. inyoensis*, in having \pm zygomorphic corollas (resulting from petal orientation vs. size differences between petals) with petals that are yellow, grading to brick-red at the tips (rarely all yellow or all brick-red) rather than some variation of white, pink,

or purple. Rollins (1993) reports two North American species of *Arabis* s.l. having yellowish white petals, *A. glabra* (L.) Bernh. and *A. missouriensis* Greene. These two taxa are taprooted biennials, very different in habit and overall morphology than *B. yorkii*. *Arabis glabra* is properly treated as *Turritis glabra*, while *A. missouriensis* is a member of *Boechera*.

Both *Boechera dispar* and *B. inyoensis* have slightly shorter sepals (4 mm) than *B. yorkii* (5 mm), as well as shorter petals. The petals of *B.*



FIG. 3. *Boechera yorkii* growing in crevice of carbonate outcrop, showing reflexed flowers and young fruit. (Photograph by Dana York).

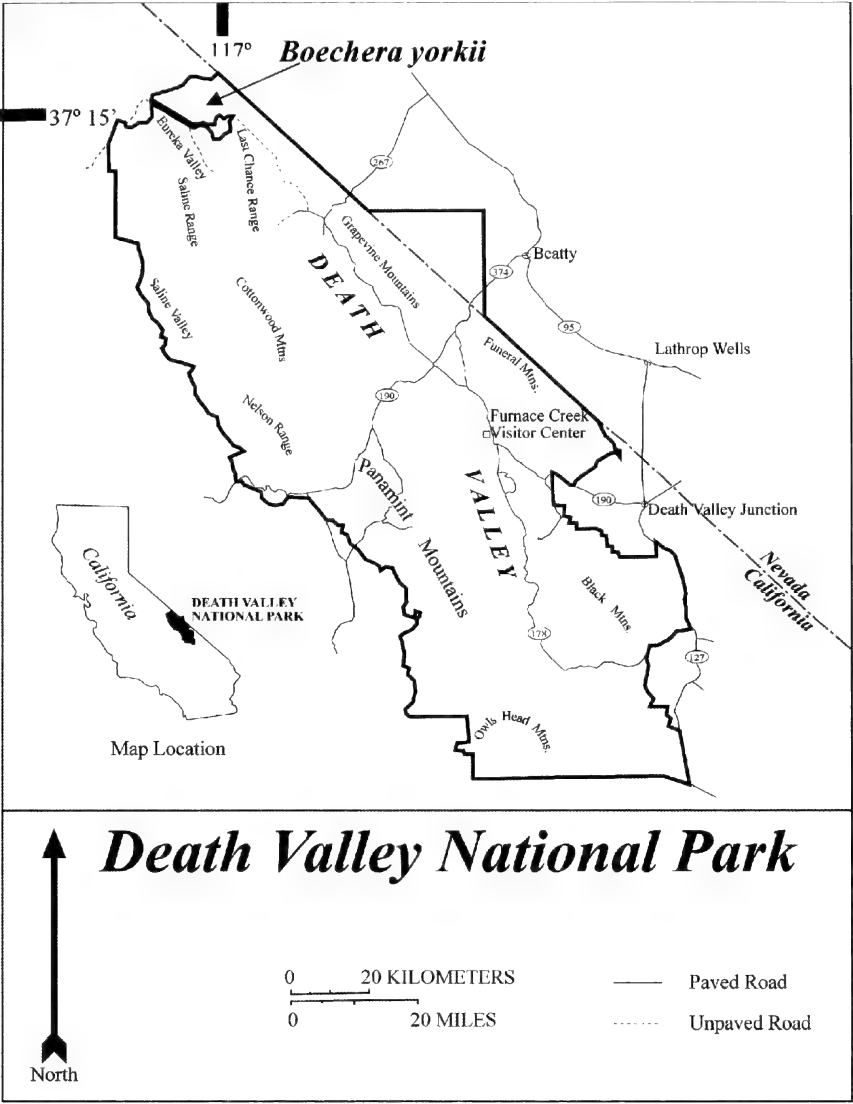


FIG. 4. Map of Death Valley National Park showing general location of the Last Chance Range and *Boecheira yorkii* population.

dispar are 5–6 mm long and those of *B. inyoensis* are 7–9 mm, while in *B. yorkii* the petals are 9–10 mm. The petals of *B. yorkii* are narrow, ca. 0.8 mm, and \pm linear, while those of *B. dispar* are ca. 2 mm wide and obovate, and those of *B. inyoensis* are ca. 2 mm wide and lingulate to spatulate.

The ovaries and young capsules of *B. yorkii* are uniformly covered with short, dendritic trichomes. Both *B. dispar* and *B. inyoensis* have young fruit which are essentially glabrous. As noted above, mature capsules of *B. yorkii* have not been documented, thus it is unclear to what extent the vestiture seen in young fruit is retained at maturity.

The pedicels of *B. yorkii* are short, ca. 1–1.5 mm at anthesis and in early fruit. Although the extent of pedicel elongation in mature fruit of *B. yorkii* is

unknown at this writing, specimens of *B. dispar* and *B. inyoensis* have much longer pedicels relative to *B. yorkii* at the same stage in early fruit. The pedicels of *B. yorkii* are sharply reflexed while those of *B. dispar* are nearly erect to divaricately ascending, and those of *B. inyoensis* spread at right angles from the stem. *Boecheira yorkii* shares with several other *Boecheira* taxa from the Death Valley region an infructescence with reflexed or descending pedicels, including *B. cobrensis*, *B. holboellii*, *B. perennans*, *B. pulchra*, and *B. sparsiflora*. From all these taxa *B. yorkii* differs in floral color, corolla symmetry, leaf vestiture, and with the exception of *B. cobrensis*, overall habit.

The only species of *Boecheira* currently known to grow sympatric with *B. yorkii* is *B. shockleyi*. Both

taxa grow in the same habitat, crevices of rock outcrops, and both are relatively scarce within the area. *Boechea shockleyi* is readily identifiable by its very dense, pannose leaf tomentum of short, stellate hairs, its long, spreading pedicels, and long, narrow, arcuate fruit. Although I considered the possibility that *B. yorkii* represents the result of hybridization between two other *Boechea* taxa, I believe it is unlikely given the relative rarity of *B. shockleyi*, and apparent absence of any other putative parental taxa within the known populations.

Boechea yorkii is a narrow endemic, restricted to the upper slopes of Last Chance Mountain in the Last Chance Range of northeastern Inyo County, California. All known populations occur within the boundaries of Death Valley National Park (Fig. 4).

Sedimentary rocks dominate the surficial geology of the Last Chance Range. *Boechea yorkii* has been found only on dolomites in the Nopah Formation, where it grows in crevices and on ledges of south-facing walls of canyons. The dolomite of the Nopah Formation is light- to medium-gray colored, with generally fine grains (McKee 1968).

Vegetation in the area where *Boechea yorkii* grows on the upper slopes of Last Chance Mountain (between ca. 2100–2545 m elevation) is a pinon-juniper woodland dominated by *Pinus monophylla* Torr. & Frém. and *Juniperus osteosperma* (Torr.) Little. Other plants associated with *Boechea yorkii* include *Allium atrorubens* S. Watson var. *cristatum* (S. Watson) McNeal, *Boechea shockleyi*, *Argyrochosma jonesii* (Maxon) Windham, *Artemisia nova* A. Nelson, *Astragalus mohavensis* S. Watson var. *mohavensis*, *A. panamintensis* E. Sheldon, *Camissonia walkeri* (A. Nelson) P.H. Raven subsp. *tortilis* (Jepson) P.H. Raven, *Cercocarpus intricatus* S. Watson, *Chaetopappa ericoides* (Torr.) G.L. Nesom, *Chrysothamnus gramineus* H.M. Hall, *C. nauseosus* (Pall.) Britton subsp. *hololeucus* (A. Gray) H.M. Hall & Clem., *Cryptantha roosiorum* Munz, *Echinocereus triglochidiatus* Engelm., *Ephedra viridis* Coville, *Ericameria nana* Nutt., *Eriogonum heermannii* Durand & Hilg. s.l., *Fendlerella utahensis* (S. Watson) A. Heller, *Gutierrezia microcephala* (DC.) A. Gray, *Lepidospartum latissquamum* S. Watson, *Leptodactylon pungens* (Torr.) Rydb., *Mimulus rupicola* Coville & A.L. Grant, *Penstemon fruticiformis* Coville s.l., *P. scapoides* D.D. Keck, *Phacelia affinis* A. Gray, *P. perityloides* Coville, *Purshia mexicana* (D. Don) S.L. Welsh var. *stansburyana* (Torr.) S.L. Welsh, *Scopolophila rixfordii* (Brandege) Munz & I.M. Johnston., *Symphoricarpos longiflorus* A. Gray, and *Tetradymia canescens* DC.

CONSERVATION STATUS

All of the known occurrences of *B. yorkii* are found within the boundaries of Death Valley National Park in a remote and relatively inaccessible area. There are no identifiable threats from human

activities, and all known populations appear secure at this time.

ACKNOWLEDGMENTS

I wish to thank Dana York for bringing this interesting new *Boechea* to my attention, for providing helpful photographs of the plant in flower and a detailed description of the plant's habitat, and for producing the map. Naomi Fraga kindly prepared and conducted an examination of pollen grains using SEM. I am especially indebted to Marisa Sripracha for making the line drawing of *B. yorkii*, work done in the evenings after having spent the previous 10–12 hours conducting floral and faunal transects on the Coachella Valley sand dunes under a blazing Colorado Desert sun, and to my son Kyle, for his assistance on a difficult, late June excursion to examine *B. yorkii* habitat in the Last Chance Mountains. Finally I thank Dr. Ihsan Al-Shehbaz and an anonymous reviewer for their insightful and helpful comments which have added much to the quality of this paper.

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REPORT OF A NEW INTRODUCED SPECIES AND REVISED KEY TO THE ANNUAL *CRASSULA* (CRASSULACEAE) OF CALIFORNIA

STEVE BOYD

Herbarium, Rancho Santa Ana Botanic Garden, Claremont, CA 91711

steve.boyd@cgu.edu

The most recent floristic treatment of *Crassula* of California (Moran 1993) and monograph of the New World annual species of the genus (Bywater and Wickens 1984) recognize four or five species in the state, respectively: *C. aquatica* (L.) Schönl., *C. connata* (Ruiz Lopez & Pavon) A. Berger, *C. saginoides* (Maxim.) Bywater & Wickens, *C. solieri* (C. Gay) F. Meigen, and *C. tillaea* Lester-Garl. Moran (1993) treats *Crassula saginoides* as a synonym of *C. aquatica*. The former four taxa are considered native to California, while the latter is an introduction from the Mediterranean basin (Bywater and Wickens 1984). Additionally, Bywater and Wickens (1984) divide *C. connata* into five varieties, of which four are reported to occur in California: *C. connata* var. *connata*, *C. c.* var. *erectoides* Bywater & Wickens, *C. c.* var. *eremica* (Jepson) Bywater & Wickens, and *C. c.* var. *subsimplex* (S. Watson) Bywater & Wickens. Moran (1993) ignores these varieties entirely. In a general sense, *C. connata* s.l. and *C. tillaea* can be considered plants of terrestrial habitats, while *C. aquatica*, *C. saginoides*, and *C. solieri* are typically associated with aquatic or emergent habitats.

In May of 2002, a local botanist, Bob Muns, brought to my attention an annual *Crassula* he had observed growing in disturbed alluvial scrub along the San Gabriel River near Irwindale, at the base of the San Gabriel Mountains in southern California. Although superficially somewhat similar to *C. connata* s.l. in overall habit, the plants in question were uniformly more robust than co-occurring individuals of *C. connata*. Muns subsequently collected fruiting specimens of the unidentified *Crassula*, and these I compared with descriptions in a number of monographic and floristic references from various arid, semiarid, and Mediterranean-climate regions of the world (e.g., Burbidge and Gray 1970; Toelken 1977; 1981; 1983; Stanley and Ross 1983; Jessop and Toelken 1986; Marchant et al. 1987), as well as with specimens housed at RSA-POM. Muns' plants bore greatest similarity to *C. sieberiana* (Schultes & Schultes f.) Druce from Australia, but also shared characters with *C. thunbergiana* J. A. Schultes, *C. campestris* (Eckl. & Zeyh.) Endl. ex Walp., *C. colorata* (Nees) Ostenf., and *C. exserta* (Reader) Ostenf. *Crassula thunbergiana* and *C. campestris* are native to southern Africa, though the former is introduced in Western Australia, while *C. colorata* and *C. exserta* are en-

demic to southern Australia (Toelken 1977, 1981, 1983). Duplicate specimens were sent to H. R. Toelken in Adelaide, South Australia, who promptly replied that the plants were consistent with *C. colligata* Toelken subsp. *lamprosperma* Toelken, an Australian taxon, one of several he had recently segregated from *C. sieberiana* s.l. (Toelken 2002, personal communication).

Crassula colligata subsp. *lamprosperma* is known from sandy to loamy soils in open woodlands, or rarely on shallow soils on or about rock outcrops, in most coastal and subcoastal areas of South Australia into adjacent areas of Victoria and Western Australia (Toelken 2002). How this taxon came to be established on disturbed alluvial terraces along the San Gabriel River in southern California remains a mystery, though I suspect one possibility could be as a contaminant in seed mix used for erosion control at the adjacent sand and gravel quarry.

At the San Gabriel River site, *C. colligata* subsp. *lamprosperma* is established over an area of at least 1–2 ha., though it is abundant in only a few local patches. Relative to *C. connata*, which is common in this area, *C. colligata* subsp. *lamprosperma* appears to favor more mesic, and disturbed microsites. In this regard it is similar to *C. tillaea*, which is also present at this site. Although it is unlikely that *C. colligata* subsp. *lamprosperma* will become a weed of significant economic or ecologic consequence, it should nevertheless be sought in other areas of California. The following key to the annual species of *Crassula* in California is provided to facilitate the effort.

1. Flowers gen. 2 per node; sepals \geq petals, tip pointed; seeds (1–)2 per carpel; plants \pm terrestrial, plants gen. not growing as submerged or emergent aquatics 2
- 1' Flowers 1 per node; sepals \pm $\frac{1}{2}$ petal length, tip rounded; seeds \geq 3 per carpel; plants gen. growing as submerged or emergent aquatics ... *C. aquatica* (incl. *C. saginoides*), *C. solieri*
2. Flowers gen. 3-merous, \pm subsessile, pedicels \ll 1.5 mm *C. tillaea*
- 2' Flowers gen. 4–5-merous, pedicels gen. $>$ 1.5 mm 3
3. Flowers gen. 5-merous; leaves gen. 4–5 mm long, \pm 1.5 mm wide, apex with short awn or mucro; sepals lanceolate, $>$ 1.5 mm long; petals lanceolate, \pm 1.2 mm long *C. colligata* subsp. *lamprosperma*

3. Flowers gen. 4-merous, leaves gen. < 4 mm long, < 1.5 mm wide, apex acute but lacking short awn or mucro; sepals triangular, < 1.5 mm long; petals narrowly triangular, < 1.2 mm long *C. connata* s.l.

Representative specimens of *Crassula colligata* subsp. *lamprosperma*: Los Angeles Co., CA. Transverse Ranges, San Gabriel Mountains Region; Santa Fe Dam Recreation Area, old San Gabriel River floodplain, on side of road leading to the Lario San Gabriel River Trail parking area, just north of Foothill Blvd. in the city of Irwindale. 28 May 2002, B. Muns s.n. (RSA, UCR, UC); Los Angeles Basin region, Vicinity of Irwindale east of the San Gabriel River and west of gravel pits, just north of Foothill Blvd, ca. 600 meters west of Irwindale Ave., near 34°8'8.8"N 117°56'19.5"W, elev. 177 m, 17 Jan 2003. S. Boyd 10441 (RSA, CAS).

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A NOTEWORTHY COLLECTION

CALIFORNIA

BERBERIS HARRISONIANA Kearney & Peebles (Berberida-ceae).—San Bernardino Co., east side of Whipple Mountains Wilderness area; just below summit of Cupcake Butte, north of Whipple Wash. Plants growing in steep talus cove between rock outcrops on northeast side of butte, north-northeast exposure. Some associated species were *Quercus turbinella*, *Acacia greggii*, *Eriogonum fasciculatum*, *Eriogonum wrightii*, *Brickellia atractylodes*, *Ephedra* sp., and *Gallium* sp. The colony was approximately 10 × 20 m. Shrubs were about 1–1.5 m high and sprawling. 34°20'47"N, 114°19'29"W, 840 m/2750 ft. Whipple Wash 7.5' quadrangle, T3N R25E center of sec. 14. 18 January 2001, John Anderson & Clif Bobinski 2001-01 (ASU, ARIZ, RSA); 10 October 2003, Sarah J. De Groot & J. Mark Porter 3308 (RSA, duplicates to be distributed); 18 March 2004, Sarah J. De Groot & Krina De Groot 3798 (RSA, RSA seed accession #21338, duplicates to be distributed).

A few additional colonies were observed farther to the north by peering over the edge of Cupcake Butte into inaccessible sites along the base of rock outcrops. This colony originally was discovered in 1998 by Clif Bobinski, outdoor recreation planner for the Bureau of Land Management, Lake Havasu Field Office.

Previous knowledge. *Berberis harrisoniana* has previously been an Arizona endemic (Kearney and Peebles 1939, Journal of the Washington Academy of Science 29(11):477–478; Kearney and Peebles 1960, Arizona Flora, University of California Press, Berkeley, CA; Shreve and Wiggins 1964, Vegetation and flora of the Sonoran Desert, Stanford University Press, Stanford, CA; Phillips et al. 1981, Status report: *Berberis harrisoniana* Kearney & Peebles, submitted to USDI U.S. Fish and Wildlife Service, Albuquerque, NM; Laferrière 1992, Journal of the Arizona–Nevada Academy of Science 26(1):2–4; Malusa 1995, Madroño 42:408–409; Whittemore 1997, Flora of North America 3:279–280; Felger 2000, Flora of the Grand Desierto and Rio Colorado of Northwestern Mexico, University of Arizona Press, Tucson, AZ).

Known populations in Arizona include the Kofa Mountains (type locality), Ajo Mountains, and Sand Tank Mountains (Arizona Rare Plant Committee 2001, Arizona Rare Plant Field Guide, Government Printing Office). Typical habitat is talus slopes and along bases of sheer cliffs, and canyons between 760 and 1100 m. These microsites are generally shady with northern exposure and more mesic than the surrounding desert (Arizona Rare Plant Committee 2001).

Significance. This is the first reported occurrence of *B. harrisoniana* in California, and the northwestern-most documented population. *Berberis harrisoniana* is a relict species related to *B. trifoliolata* Moric. from southeastern Arizona, New Mexico, and Texas. It has a disjunct distribution pattern with few scattered occurrences in desert mountain ranges of southwestern Arizona and now adjacent California.

—JOHN ANDERSON, Bureau of Land Management, Phoenix Field Office, 21605 N. 7th Avenue, Phoenix, AZ 85027-2099; SARAH J. DE GROOT, Rancho Santa Ana Bo-

tanica Garden, 1500 N. College Avenue, Claremont, CA 91711. sarah.degroot@cgu.edu.

CALIFORNIA

CRATAEGUS CASTLEGARENSIS J. B. Phipps & O'Kennon (ROSACEAE).—Modoc Co., near shore of Egg Lake, Jun–Aug 1893, M. S. Baker s.n. (POM); Shasta Co., on Hat Creek, ca. 32 km W of Fall River Mills, 24 May 1940, C. L. Hitchcock 6558 (POM, RSA); Shasta Co., Fall River Lake, 5 Aug 1899, M. S. Baker s.n. (POM); river bank, moist rocky loam, N aspect, along the Fall River, 1.6 km NW of Fall River Mills, elev. 975 m, with *Juniperus occidentalis* Hook., 25 Jul 1941, C. B. Wolf 11071 (POM, RSA).

Previous knowledge. Castlegar hawthorn was recently described, with a range from Wyoming to British Columbia, south to central Oregon and northeastern Utah (Phipps and O'Kennon 2002, Sida 20:115–144). It is a native black-fruited shrub in a complex of similar species. Often some thorns on a plant of *C. castlegarensis* will be paired (or tripled), an unusual but not unique feature in western members of the genus. *Crataegus castlegarensis* has pubescent pedicels and subglobose to depressed-globose fruits, but otherwise is similar to native *C. douglasii* Lindl., which has glabrous pedicels and more ellipsoid fruits that ripen a month earlier. Leaf venation, long slender thorns (mostly 2–3 cm), and flowers with 8–10 stamens separate both from *C. suksdorfii* (Sarge.) Kruschke, the third native hawthorn in California. *Crataegus suksdorfii* has short stout thorns (always less than 1.8 cm) and 16–20 stamens per flower.

Significance. First report for California. Disjunct 350 km from nearest recorded populations in Grant Co., Oregon.

—PETER F. ZIKA, Herbarium, Burke Museum, Box 355325, University of Washington, Seattle, WA 98195-5325. Zikap@aol.com.

OREGON

BIDENS CONNATA Muhl. ex Willd. (ASTERACEAE).—Clatsop Co., weed in cultivated cranberry field, N end of Delmar Loop Road, W of Cullaby Lake, 4 m, 2 Oct 1999, Zika 14458 (OSC, WTU); Columbia Co., disturbed seasonally wet ground, full sun, near S shore of Columbia River, SE end of Diblee Point, 5 m, 23 Sep 2003, Zika 19106 (OSC, UBC, WTU); Curry Co., cranberry bogs and the dikes around them, Sea Winds Farm, 0.3 km N of Cape Blanco, 60 m, 6 Oct 1997, Wilson 9068 (OSC).

Previous knowledge. Purple-stem beggarticks is native to eastern North America, west to Nebraska. It is adventive in British Columbia and Washington.

Significance. First collections for Oregon.

JUNCUS DIFFUSISSIMUS Buckley (JUNCACEAE).—Columbia Co., disturbed seasonally wet ground, full sun,

near S shore of Columbia River, SE end of Diblee Point, 5 m, 23 Sep 2003, *Zika* 19107 (OSC, WTU).

Previous knowledge. Slimpod rush is native to the southeastern United States. It is known as a weed in California and Washington.

Significance. First report for Oregon.

WASHINGTON

CERASTIUM BRACHYPETALUM Pers. subsp. *BRACHYPETALUM* (CARYOPHYLLACEAE).—Asotin Co., sand and cobble W bank of Snake River, with *Cerastium glomeratum* Thuill., *C. pumilum* Curtis, 0.8 km SE of Asotin, 230 m, 15 May 2003, *Zika* 18363 (MICH, WS, WTU).

Previous knowledge. Gray mouse-ear is native to Europe, and has been reported as a weed in the eastern United States and Oregon (R. R. Halse 2003, Madroño 50: 215-216).

Significance. First report for Washington.

HIERACIUM × *FLAGELLARE* Willd. (ASTERACEAE).—San Juan Co., common in dry ground, meadow, S end of airstrip, Mt. Baker Road, N end of Orcas Island, 10 m, 13 Jun 2003, *Zika* 18466B (STU, WS, WTU).

Previous knowledge. Whip hawkweed is usually treated as a stabilized hybrid between the European species *Hieracium caespitosum* Dumort. and *H. pilosella* L. It is a weed in eastern North America, as well as British Columbia. It is often found in situations without either parent.

Significance. First report for Washington.

HYPERICUM TETRAPTERUM Fr. (CLUSIACEAE).—Wahkiakum Co., rooted on drift logs, freshwater intertidal marsh, mouth of Deep River, N end of Grays Bay, Columbia River, 1 m, 24 Sep 2003, *Zika* 19145 & *C. Maxwell* (UC, WTU); weed in sunny disturbed ground by driveway, SW end of Waranka Road, N end of Grays Bay, 2 m, 24 Sep 2003, *Zika* 19146 & *C. Maxwell* (WTU).

Previous knowledge. Square-stalked St. Johnswort is native to Europe. I am aware of only one prior report from North America. It is a weed 350 km to the north in Vancouver, British Columbia (F. Lomer 1997, The genus *Hypericum*—St. John's wort—in British Columbia, Botanical Electronic News 166:1-4. <http://www.ou.edu/cas/botany-micro/ben/>).

Significance. First collection for Washington.

LEPIDIUM BONARIENSE L. (BRASSICACEAE).—Skagit Co., dirt heaps on dike, near boat ramp, N bank of Skagit River, 10 m, 21 Jun 2003, *Zika* 18504 (MO, UC, WTU); dirt heaps near Burlington Boulevard bridge, N shore of Skagit River, Burlington, 10 m, 22 Jun 2003, *Zika* 18507 (MO, WTU); dirt roadside, near railroad and soccer fields, Skagit Park, Burlington, 10 m, 21 Jun 2003, *Zika* 18503 (UBC, WTU); Whatcom Co., grassy bank, N side of Slater Road, 2 air km SE of Tennant Lake, 10 m, 26 Sep 2003, *Zika* 19168 (WTU).

Previous knowledge. Argentinean pepperwort is native to South America, and has been naturalized on the big island of Hawai'i since 1975 (W. L. Wagner, D. R. Herbst, and S. H. Sohmer, 1999. Manual of the flowering plants of Hawai'i, Revised Ed., Vol. 1. Bishop Museum Special Publication 97). *Lepidium bonariense* has also been col-

lected as an adventive on wool waste in South Carolina. Rollins (1993, The Cruciferae of Continental North America, Stanford University Press, Stanford, CA) mentioned the species, but was uncertain that it was truly established in North America. In northwestern Washington there are some sizeable populations, suggesting it has been naturalized for some time. It is easily overlooked, closely resembling the common *Lepidium virginicum*, but differing in its pinnatifid bracteal leaves.

Significance. First collections for Washington.

MALUS × *DAWSONIANA* Rehder (ROSACEAE).—Clark Co., common hybrid with parents, shrub-invaded wet prairie remnant, NE Ward Road, historic Fifth Plain Creek floodplain, 70 m, 5 May 2003, *Zika* 18320 (WTU); thickets at edge of meadow, Allen Canyon Road, 4 air km NE of Ridgefield, 70 m, 27 Aug 2003, *Zika* 18919 (WTU); thickets near pondshore, Madina Park, Madina, 20 m, 28 Aug 2002, *Zika* 17715 & A. L. Jacobson (WTU); forested strip by golf course, S end of Green Lake, Woodland Park, Seattle, 50 m, 4 May 2002, *Zika* 16834 (WTU); Thurston Co., thickets in prairie remnant, with parents, Scatter Creek Wildlife Area, 60 m, 15 Oct 2001, *Zika* 16692 & F. Weinmann (WTU).

Previous knowledge. Hybrid Pacific crabapple is a rare cross between native *Malus fusca* (Raf.) Schneid. and introduced *Malus domestica* Borkh. It was described from a seed source in Oregon, and is rarely cultivated (A. L. Jacobson 1996, North American landscape trees, Ten Speed Press, Berkeley, CA.; A. L. Jacobson 2001, Wild plants of Seattle, Publ. by the author, Seattle, WA.). All Washington records are believed to be spontaneous hybridizations, not escapes from gardens. Wild plants are extant in northwestern Oregon, in the lower Willamette (*Zika* 18259 WTU) and Columbia River (*Zika* 18409 OSC) drainages; 75 km to the south. The hybrid is intermediate between the parents in leaf lobing, floral characters, and fruit. It is easily overlooked, but can be detected in bloom by the slightly corymbiform inflorescence, with flowers too large for *M. fusca*. Fruits are longer than wide, as in *M. fusca*, but 2-4 cm long, and thus considerably smaller than wild *M. domestica*, which has fruits wider than long. C. A. Huckins (1968, *Baileya* 15:129-164) claims the inner wall of the fruiting carpel is lined with a soft whitish outgrowth, but we have not seen this on any hybrids or the parents.

Significance. First collections for Washington.

POPULUS × *CANESCENS* (Aiton) Sm. (SALICACEAE).—Thurston Co., male clone, hundreds of stems, invading prairie remnant, South Unit of Scatter Creek Wildlife Area, Mound Prairie, 55 m, 14 May 2003, *Zika* 18350 (WTU).

Previous knowledge. Gray poplar is a hybrid between *Populus alba* L. and *P. tremula* L., both native to Europe. The cross is occasionally cultivated as an ornamental in western Washington, and is recorded as a wild plant in British Columbia. *Populus* × *canescens* is a widespread adventive in eastern North America, in the absence of its parents.

Significance. First report as a garden escape in Washington.

SENECIO CINERARIA DC. (ASTERACEAE).—San Juan Co., adventive on cliff face, 3 m above ground level, with

cultivated plants in vicinity; near ferry landing, Orcas Island, San Juan Islands, Puget Sound, 5 m, 13 Jun 2003, Zika 18474 & Jacobson (WTU).

Previous knowledge. Silver ragwort is native to the Mediterranean, and occasionally cultivated. It is reported as a weed in Oregon and California.

Significance. First collection as a garden escape in Washington.

—PETER F. ZIKA, Herbarium, Burke Museum, Box 355325, University of Washington, Seattle, WA 98195-3525. Zikap@aol.com.

WASHINGTON

TYPHA DOMINGENSIS Persoon (TYPHACEAE). Adams Co., ca. 8 km north of Othello on the north shore of Herman Lake, 46°54.193'N 119°11.866'W, elev. ca. 300 m, on mud or in water to ca. 20 cm deep, associated with *Schoenoplectus pungens*, *Potamogeton nodosus*, *Chara* sp., and *Juncus* sp., 10 July 2001, J. Parsons and B. Dickes 378 (WTU); *Typha domingensis* and *T. domingensis* × *T. latifolia*, ca. 10 km northwest of Othello on the shoreline of Hutchinson Lake, 46°52.637'N 119°17.845'W, elev. ca. 300 m, on mud or in water to ca. 30 cm deep, associated with *Schoenoplectus acutus*, *Lythrum salicaria* and *Phragmites australis*, 27 August 2001, J. Parsons 378a and 378b (WIS). Both lakes are in the channeled scablands of central Washington State. The lakes were created in the 1950's as part of the Columbia River Irrigation Project.

Previous knowledge. *Typha domingensis* is a pan-tropic to warm temperate species that commonly occurs to 40° north and south latitude throughout the world. It is widespread in the United States within that range (S. G. Smith, Typhaceae, pp. 278–285 in Flora of North America Editorial Committee, Flora of North America North of Mexico, vol. 22, 2000).

Significance. First record for Washington State. Extends the known range of plants that have been definitely identified as *T. domingensis* ca. 400 miles to the north from northern California (Del Norte and Lassen Counties). A northwestern Wyoming (Hot Springs Co.) collection from ca. 550 miles to the southeast in a hot spring is a possible *T. domingensis* × *T. latifolia* hybrid. The previously known northernmost North American collection which is definitely *T. domingensis* is from northern Illinois at about 42°N and is from a power plant cooling pond. The Washington colonies of *T. domingensis* and *T. domingensis* × *T. latifolia* are on the shores of two lakes in a region of many lakes, wetlands and canals south of Potholes Reservoir. There is significant *Typha* habitat in this region, and it is likely that additional colonies of *T. domingensis* and putative hybrids occur in the vicinity. It seems likely that the seeds of *T. domingensis* and putative hybrids were carried to Washington by waterfowl on their northern migration from California, where *T. domingensis* is common in the Central Valley and where *T. domingensis* × *T. latifolia* hybrid seeds are probably often produced (S. G. Smith, Experimental and natural hybrids in North American Typha (Typhaceae). Amer. Midl. Naturalist 78: 257–287. 1967). The Washington plants are producing many inflorescences with apparently mature fruiting spikes, but seeds are present only in the *T. domingensis* specimens collected in late August, the seed-set is less than 50%. The seeds are apparently not completely mature. The absence of

seeds is expected in the putative hybrids, but the apparently non-hybrid plants should be seed-fertile. It seems likely that the absence of mature seeds at the Washington localities is due to the relatively short growing season or to the different photoperiod regime. Even in the absence of mature seeds, the *T. domingensis* and putative hybrid plants at the sites in Washington are likely to persist and spread by means of rhizomes.

—JENIFER K. PARSONS, Washington Department of Ecology, 15 W Yakima Ave., Yakima, WA 98902; S. GALEN SMITH, Department of Biological Sciences, University of Wisconsin-Whitewater, Whitewater, WI 53190. jenp461@ecy.wa.gov.

WASHINGTON AND BRITISH COLUMBIA

SCUTELLARIA ANGUSTIFOLIA subsp. *MICRANTHA* Olmstead (LAMIACEAE). Ferry Co. (WA), Colville National Forest, Bodie Mountain, west of primitive road, about 15 m down from Bodie Peak. Corollas deep blue with white stamens. Growing in thin soil and bare basalt with *Eriophyllum lanatum*, *Poa sandbergii*, *Pseudotsuga menziesii*, *Penstemon* sp., *Artemisia* sp., *Eriogonum* sp., *Heuchera* sp., *Sedum* sp. T38N, R32E, Sect. 6, NW1/4, 1750 m elevation, 9 Jul 1999, Robohm 99-18 (WTU, OSC); Pend Oreille Co. (WA), Colville National Forest, about 6.5 km east of Usk. Take County Road 9216 northeast from Usk 2 km to County Road 9305, follow 9305 for 3 km to County Road 3266. Hike up ridgeline then drop down to 850 m elevation. Growing in *Festuca idahoensis*/*Pseudoroegneria spicata* community with *Pinus ponderosa*, *Danthonia uniflora*, *Balsamorhiza sagittata*, *Eriogonum heracleoides*, *Bromus japonicus*, and *Phlox diffusa*. T33N, R44E, Sect. 35, elevation 850 m, 19 Jun 1996, Karen Larson and Monica Hunt 65 (WTU, OSC); Okanogan-Similkameen District (British Columbia), 4 km west of the town of Midway, about 1.7 km north of the U.S.A. border. Kettle River valley, north side, about 300 m north of truck weigh scales, Highway 3 Alt. Dry stable talus cliff base above weedy field on ponderosa pine slope, growing between rocks, probably basalt. Associated with *Clarkia pulchella*, *Phacelia hastata*, *Hackelia ciliata*, *Ipomopsis aggregata*. Population spread over 20 m² patch with five clumps per m². Also occurs 5 km to east where it is probably more abundant (above cemetery at Midway). Elevation 640 m. Frank Lomer 98-80 (WTU).

Previous knowledge. *Scutellaria angustifolia* Pursh is divided into two subspecies possessing rather distinct distributions. *S. angustifolia* subsp. *angustifolia* occurs in the northern half of Oregon along the east slope of the Cascades and the east end of the Columbia River Gorge, in central Idaho primarily along the Snake, Salmon, and Clearwater rivers, and in northern Idaho and eastern Washington to the Canadian border, with one collection known from adjacent British Columbia; *S. angustifolia* subsp. *micrantha* occurs in Nevada's northern Great Basin and in southeastern Oregon eastward across the Snake River plains to central Idaho, with outlying collections in the foothills of Utah's Wasatch Mountains (R.G. Olmstead, Contributions from the University of Michigan Herbarium 17: 223–265, 1990). Both taxa show an affinity for basalt-derived substrates.

Significance. These three collections extend the northern range of *S. angustifolia* subsp. *micrantha* by nearly

1000 km. The collections represent the northernmost populations in the U.S., and the only vouchered population in Canada. The collection localities share ecological features consistent with those found in the taxon's more southerly distribution: xeric conditions and thin basaltic soils. These collections raise interesting questions regarding this taxon's distribution. It is unclear whether these populations arose through long-distance dispersal or are relictual from a previously continuous distribution linking the arid in-

terior Pacific Northwest with the Great Basin. The Washington Natural Heritage program tracks this taxon under the status of Review Group I, and in Canada its status is under review.

—DAVID GIBLIN, RICHARD G. OLMSTEAD, University of Washington Herbarium, Burke Museum, Box 355325, University of Washington, Seattle, WA 98195-5325. dgiblin@u.washington.edu.

REVIEWS

Vegetation of circumboreal coniferous forests. Edited by Milan Chytrý and Toby Spribille. 2002. OPULUS Press, Uppsala, Sweden. 184 pp. EUR 30.00. ISBN 91-88716-27-9.

The coniferous forests of Eurasia and North America represent one of the largest vegetation formations in the world, occupying approximately 19 million km². The centers of biodiversity of these forests are in eastern Asia and western North America. However, despite their vast size and environmental significance, boreal forests have received comparatively little attention from phytosociologists. Their continuous distribution across the northern hemisphere points to the need for international cooperation in comparative studies and prioritization of particular areas for conservation. In order to facilitate such cooperation, a workshop entitled “Vegetation Classification and Phytogeography of Circumboreal Coniferous Forests” was held in association with the 44th Symposium of the International Association for Vegetation Science in Freising-Weihenstephan, Germany, in 2001. The volume under review took shape at this workshop. It proves that finding a common platform for an understanding of the circumboreal coniferous biome is a realistic goal.

Representation of relevant geographical areas is reasonably balanced: two chapters on European coniferous forests, two on forests in Asia, and two on forests in British Columbia, the American Northwest, and the Rocky Mountains. Toby Spribille and Alina Stachurska-Swakon wrote chapters on classification of North American coniferous forests. As it has already been apparent from his earlier writings (1999, 2000, 2001), Spribille emerges as a leader in American phytosociology. His elaborated descriptions of forest communities (bryophytes and lichens are included) and their classification into floristically defined associations, alliances, and orders match international standards and follow rules of the International Code of Phytosociological Nomenclature (Weber et al. 2000). In the two mentioned chapters, over 700 relevés were used for identification of 35 associations of which 13 were described for the first time. Also, one new alliance and one new order were validly published here. We should appreciate validation of several old names in these chapters. This is a commendable habit that helps to maintain links to earlier studies and prevents accumulation of unnecessary synonyms.

The only critical comment that I can make is probably not completely fair at this stage of development of phytosociology in North America (and,

for the same reason in Asia), but it still should be spelled out: more attention should be paid to soil and climate characterization of individual syntaxa. So far, qualitative statements about soil moisture, longitudinal and altitudinal range, slope, and cover in individual strata is usually all what is provided. In Europe, phytosociology has been walking hand in hand with soil science since the very beginning when Josias Braun-Blanquet started working with Hans Jenny in the Alps in the early 1920's.

Currently, an unresolved issue is whether boreal coniferous forests in North America belong to the class (the highest vegetation classification unit) *Vaccinio-Piceetea*, originally described by Braun-Blanquet and his colleagues from the Alps. Many circumboreal elements of these forests (*Galium boreale*, *Linnaea borealis*, *Listera cordata*, *Lycopodium* spp., *Moneses uniflora*, *Orthilia secunda*, *Pleurozium schreberi*, *Rhytidadelphus loreus*, *Vaccinium uliginosum*, etc.) provide the justification for one circumboreal class. However, the paucity of traditional *Vaccinio-Piceetea* species in the forests of the alliance *Tsugion mertensianae*, known from subalpine habitats in Oregon, Idaho and British Columbia, makes this question more complicated.

The chapter by Milan Chytrý (Czech Republic) and his colleagues from Austria and Slovakia deals with the Central European *Picea abies* forests. This chapter deserves a special attention. It addresses a nagging question of inconsistent approaches to the designation of diagnostic species. Using 20,164 relevés from the Central European forests, they concluded that lists of diagnostic species published in phytosociological literature are heavily context-dependent. Some of these lists are useful for identification of vegetation units at a local scale, while others for distinguishing units within a narrowly delimited community type over a large area. Therefore, the application of published lists of diagnostic species outside of the context (the underlying data sets and range of comparisons) should be done only with an explicit understanding of this context.

Two recent attempts to classify vegetation in the western United States have been, for many different reasons, unsatisfactory; for critical evaluations see Keil (1997), Rejmánek (1997), Zedler (1997), and Spribille and Česka (2002). As a contrast, North American studies in this volume, as well as studies by Manuel Peinado and his colleagues (1997, 1998), represent a definitive starting points of, and models for, professional vegetation classification in this part of the world. Because now, after a long period of neglect, the need for vegetation classification is clearly recognized in the U.S. (

www.esa.org/vegweb/docFiles/NVC_Guidelines.v40.pdf), this volume should be available, at least, in all professional libraries.

—MARCEL REJMÁNEK, Section of Evolution and Ecology, University of California, Davis, CA 95616. mrejmanek@ucdavis.edu.

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Plant invasions: ecological threats and management solutions. Edited by L. Child, J. H. Brock, G. Brundu, K. Prach, P. Pyšek, P. M. Wade, and M. Williamson. 2003. Backhuys Publishers, Leiden, the Netherlands. xii + 457 pp., 106 figures, 84 tables. Paperback, Euro 108.00. ISBN 90-5782-135-4.

California is definitely one of the states where interest in invasive plant species has a long tradition (Parish 1920; Robbins 1940; Baker 1962; Frenkel 1970; Randall et al. 1998), and there are many reasons for that (Bossard et al. 2000). Therefore, any interesting publication on plant invasions should be a welcome contribution to our institutional and, as far as we can afford, our private libraries. The book under review is one of them. This volume presents key contributions from the 6th International Conferences on the Ecology and Management of Alien Plant Invasions (EMAPi) held in Loughborough, U.K., in September 2001. In total,

30 chapters were written by 64 authors from 22 countries and 5 continents. The volume is divided into six sections: 1) Mechanism and impact (five chapters), 2) Alien floras (six chapters), 3) Species ecology: congeners (six chapters), 4) Case studies (five chapters), 5) Control (four chapters), and 6) Management (four chapters).

Initially, we may be somewhat disappointed as only one contribution is from the USA (J. H. Brock: *Elaeagnus angustifolia* seed banks from invaded riparian habitats in northeastern Arizona). Nevertheless, as has been already stressed many times, plant invasions are a global problem, and we can learn a lot from what is going on in Argentina, Australia, Europe, or New Zealand. Moreover, several contributions in this volume are of general importance, addressing very basic questions of invasion biology. Just a few examples: (1) Understanding patterns of plant invasions at different spatial scales (10 km² to >1,000,000 km²) (M. Rouget and D. M. Richardson): environmental factors best explained distribution at broad scales; whereas, propagule pressure explained most of the variation at finer (local) scales. (2) The introduction of American plant species into Europe (J. Forman): based on a 6000-species database and the strong relationship between weediness in America and likelihood of being non-benign in Europe, a warning list was compiled to assist European policy makers in preventing future invasions. Not surprisingly, several American species of *Amaranthus*, *Bidens*, *Conyza*, and *Solanum* are on this list; however, *Xanthium strumarium* that is listed here as well, was introduced to Europe not from America but from its native range in East Asia in the Bronze Age. (3) Invasion of the Portuguese dune ecosystems by *Acacia longifolia* (H. Marchante, E. Marchante, and H. Freitas): this Australian species was introduced for dune stabilization; plots invaded by this species have significantly lower species richness than uninvaded patches of native vegetation. As *A. longifolia* is also a difficult invader in coastal areas of South Africa, we should watch this species in California. (4) Alien flora of the Czech Republic (P. Pyšek, J. Sadlo, and B. Mandak): a catalogue of 1378 alien plant taxa (Pyšek et al. 2002), which currently serves as one of the best available models for other countries, is re-analyzed here and compared with relevant information from the British Isles. (5) Japanese knotweed (*Fallopia* spp.) at home and abroad (J. Bailey, C. H. Pashley, and C. Ferris): hybridization and backcrossing is an important phenomenon, offering the possibility of the production of populations better suited for new environments. (6) Invasiveness of 15 *Oenothera* congeners in Europe related to seed characteristics (S. Mihulka, P. Pyšek, and J. Martinkova): germination characteristics appear to be more important than other attributes; taxa that tend to germinate easily in the light are the best invaders. (7) Biological control of invasive weeds in the UK (R. H. Shaw): despite over 1000 releases

of weed biological control agents around the world, the UK and Western Europe have never undertaken a full biological control program against a weed target; currently the top potential biocontrol targets include *Fallopia japonica*, *Heracleum mantegazzianum*, *Impatiens glandulifera*, *Rhododendron ponticum*, *Hydrocotyle ranunculoides*, *Myriophyllum aquaticum*, and *Buddleja davidii*.

My impression is that studies reported in recent EMAPi volumes are becoming more sophisticated, and the overall quality is increasing. Despite this progress, one chronic weakness of plant invasion biology still remains: a lack of rigorous evidence for assumed harmful impacts of invasive taxa. The phrase “ecological threats” is used in the title of this volume, but only a few contributions touch on this topic. Even if mostly demagogic and based on half-truths, some critical comments made recently by Theodoropoulos (2003) should be taken seriously. Clearly, a more balanced view is what we need (Sax and Gaines 2003).

—MARCEL REJMÁNEK. Section of Evolution and Ecology, University of California, Davis, CA 95616.

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Introduction to shore wildflowers of California, Oregon, and Washington. By Philip A. Munz, and edited by Dianne Lake and Phyllis M. Faber. 2003. Revised edition. California natural history guides v. 67. University of California Press, Berkeley, CA. 234 pp. \$39.95 cloth, \$16.95 paperback. ISBN 0-520-23639-4.

Introduction to California mountain wildflowers. By Philip A. Munz, and edited by Dianne Lake and

Phyllis M. Faber. 2003. Revised edition. California natural history guides v. 68. University of California Press, Berkeley, CA. 247 pp. \$39.95 cloth, \$16.95 paperback. ISBN 0-520-23637-8.

Introduction to California plant life. By Robert Ornduff, and revised by Phyllis M. Faber, and Todd Keeler-Wolf. 2003. Revised edition. California Natural History Guides v. 69. University of California Press, Berkeley, CA. 341 pp. \$39.95 cloth, \$16.95 paperback. ISBN 0-520-23704-8.

Pests of the native California conifers. By David L. Wood, Thomas W. Koerber, Robert F. Scharf, and Andrew J. Storer. 2003. California Natural History Guides v. 70. University of California Press, Berkeley, CA. 233 pp. \$48.00 cloth, \$19.95 paperback. ISBN 0-520-23329-8.

Dragonflies and damselflies of California. By Tim Manolis. 2003. California Natural History Guides v. 72. University of California Press, Berkeley, CA. 201 pp. \$39.95 cloth, \$16.95 paperback. ISBN 0-520-23567-3.

As part of a new publishing initiative, the University of California Press has undertaken an effort to update the California Natural History Guides series. Five recently released volumes include three that are revisions of previously published guides (*Introduction to shore wildflowers of California, Oregon, and Washington*; *Introduction to California mountain wildflowers*; *Introduction to California plant life*), and two new guides (*Pests of the native California conifers*; *Dragonflies and damselflies of California*). First launched 45 years ago in the midst of changing population demographics that had resulted in an influx of residents unfamiliar with the flora and fauna of their new surroundings, the objective of the original California Natural History Guide Series was to “foster an understanding and enthusiasm, among a broad range of readers, of the flora, fauna, and natural features of California and of the ecological interrelationships of species, communities and habitats.” California continues to attract newcomers in large numbers and the need for accessible natural history information remains just as, or even more, important and relevant today.

Both the *Introduction to shore wildflowers of California, Oregon, and Washington*, and the *Introduction to California mountain wildflowers* have been updated with new information, and revised scientific names in accordance with *The Jepson manual: higher plants of California*. Only a portion of the rich flora of these two regions can be represented, but an attempt was made to include the most common and widespread species. Among the featured species are several exotics, which have become a larger part of our flora since the first editions were published. While many of the original line drawings have been retained, both books contain an abundance of new high quality photographs.

Species are listed in no particular order by flower color and the guides do not contain keys, making these guides best suited to novice enthusiasts. Stouter construction corrects the tendency of the bindings of some of the older editions to fall apart, thus making them more durable for field use.

First published in 1974, the new edition of *Introduction to California plant life* provides an overview of factors, both physical and biological, shaping plant pattern and distribution, plus a description of the different vegetation types found in the state. Two of the original seven chapters have been expanded and split, while a chapter on early explorers and plant collectors was added. This new chapter provides an interesting reminder of how many of our plants got their scientific names. Some material is a bit specific for an introductory book, but the addition of many excellent new photographs enhances the appeal to a diverse readership.

The two new entomological guides are geared more towards professional resource managers or serious enthusiasts. From the early pages where the authors' explain the concept of a pest species, to the glossary of biology and forestry related terms, *Pests of the native California conifers* is well assembled and of high diagnostic and educational value. The guide contains substantial information regarding damage to conifers from insects, from biotic and abiotic diseases, as well as from larger animals. Professionals will find this guide useful as a quick reference for verifying causes of injury. Novices will also find the *Pests of the native California*

conifers to be a good introduction to diagnosing damage to conifers due to the extensive and high quality color plates, and from the descriptions that point the reader toward species that produce similar types of damage. The quick reference guides to damage by symptom location and by host species are valuable tools for sorting through possible causes of damage and make this guide a very user-friendly choice for anyone interested in identifying pests of California conifers.

Complete and well illustrated, the *Dragonflies and damselflies of California* will benefit both novice and experienced naturalists with an interest in this fascinating group of insects. The straightforward introduction explains the life history and behavior of the order Odonata, to which dragonflies and damselflies belong, while offering useful tips for watching and identifying Odonates in the field. This guide is well rounded and includes easily accessible keys to families and subfamilies for those interested in learning more about Odonate taxonomy. The "similar species" sections of the species accounts will vastly improve the Odonate identification skills of the less experienced. In future editions, the species accounts section of the guide would benefit from a more distinctive system of color coding or quick referencing.

—ERIC KNAPP, U.S. Forest Service Pacific Southwest Research Station, Redding, CA 96002. eknapp@fs.fed.us.
SCOTT FERRENBURG, U.S. Geological Survey, Western Ecological Research Center, Sequoia and Kings Canyon Field Station, Three Rivers, CA 93271.

ANNOUNCEMENT

CALIFORNIA BOTANICAL SOCIETY
2004–2005 SCHEDULE OF SPEAKERS

All meetings are held at 7:30 pm, on the 3rd Thursday of the month (except February)

Room 2063 Valley Life Sciences Building
University of California, Berkeley

- | | |
|--------------------------|--|
| September 16, 2004 | Raymond Cranfill, University Herbaria, University of California, Berkeley The secret life of ferns |
| October 21, 2004 | James Wanket, Department of Geography, Sacramento State University Relicts and refugia: late Quaternary forests of the Klamath Mountains |
| November 18, 2004 | Susan Lambrecht, Department of Environmental Studies, University of California, Santa Cruz The cost of flowers in ecological currencies |
| January 20, 2005 | James Shevock, National Park Service, Cooperative Ecosystem Studies Unit, University of California, Berkeley Bryogeography of California: what can we learn from the mosses about past and future climate changes? |
| February 19, 2005 | Annual Banquet, Romberg Tiburon Center, Tiburon, CA Arturo Gómez-Pompa, Department of Botany and Plant Sciences, University of California, Riverside Center for Tropical Research (CITRO): a new initiative in a time of crisis |
| March 17, 2005 | Scott Stephens, Department of Environmental Science, Policy and Management, University of California, Berkeley Dynamics of the last, intact, Jeffrey pine ecosystem from northwest Mexico: U.S. restoration implications |
| April 21, 2005 | Elizabeth Wenk, Department of Integrative Biology, University of California, Berkeley Effect of differing substrates on plant physiology and distribution in the alpine Sierra Nevada |
| May 19, 2005 | Michelle McMahon, Department of Evolution and Ecology, University of California, Davis Diversification of floral development in the papilionoid legume tribe Amorpheae |

Seminars are open to all. Refreshments will be served following all seminars.

NOTE CORRECTED DATES FOR OCTOBER AND NOVEMBER SEMINARS

PRESIDENT'S REPORT FOR VOLUME 51

Reflecting on last year's report for Volume 50, I immediately notice a big difference. No snow on the ground. In fact, summer is just ending and we have not yet passed the fall equinox. Volume 51(4) will likely arrive before the snow flies, a milestone indeed. Last year, we were ecstatic to be *almost* back on time. This year, *Madroño* actually is *ahead* of schedule. This achievement is the culmination of years of dedicated effort, led by Editor John Callaway and reinforced by a succession of *Madroño* editorial contributors including Editorial Assistant Laura Wainer, Book Editor Jon Keeley, Noteworthy Collection Editors Dieter Wilken and Margriet Weatherwax, and all of the members of the Board of Editors. It also reflects the effort of our past council, led by the vision and energy of past president Bruce Baldwin. And, lastly, it underscores the fact that *Madroño* is still attracting quality manuscripts and that the practice of botany, in the broad sense, is still alive and well. Ultimately, it is the work of all of you that keeps *Madroño* a viable scientific journal and an indicator of the health of the California Botanical Society.

Nonetheless, John Callaway deserves recognition and our enduring appreciation for his exemplary work as Editor during this past three years. And, in fact, he got it! One of the highlights of society activities in 2004 was our annual banquet in February held at the historic Log Cabin facility at the Presidio in San Francisco. During the evening's festivities, John was given a beautiful framed print of the Sierras as a token of our appreciation for his contribution as *Madroño* editor. Mark Brunell, past second vice president, is to be commended for his excellent job in organizing this event. Our hosts were members of the natural resource management staff of the Presidio Trust. I particularly wish to thank Terry Thomas of the Presidio Trust for her hospitality and support for this function. Earlier in the day, Presidio Trust biologists Katrina Strathman, Mark Frey, and Michael Chassez hosted a tour of state-of-the-art habitat restoration and sensitive species management activities that are taking place in this urban biodiversity hot-spot. Council members Dean Kelch and Staci Markos created elegant floral table settings that much contributed to the festive atmosphere. Along with John Callaway, we also acknowledged the great job that Bruce Baldwin did during his tenure as our immediate past president. Bruce's professionalism and generous spirit lifted the society through some challenging times and we are very fortunate to have had Bruce as president of the society.

Our distinguished speaker at the banquet was Dr. Hal Mooney. Hal spoke on "A Personal View of California Plant Ecology: Past, Present, and Future." Although hard to imagine given his youthful appearance and enthusiasm, Hal chronicled his personal observations of some of the great ecologists in California history and highlighted a past tendency for them to move east once their careers became established. Times have changed. Today, centers of ecology in California, such as the "wilderness" at UC Davis, have become magnets for some of the world's finest ecologists, as are numerous other UC institutions, CSU campuses, non-profit organizations (such as the Nature Conservancy), and natural resource management agencies. Ecology is alive and well in the Golden State.

Other highlights of 2004 included an excellent public

lecture series organized by Second Vice President Stefania Mambelli. These free lectures are held in the Valley Life Sciences Building at UC Berkeley (7:30 p.m. on the third Thursday of every month, excluding February and the summer months). Thanks to our speakers: Walter Koenig, Jeff Corbin, Gretchen LeBuhn, Michael Loik, Will Russell, Jean Langenheim, and Nishi Rajakaruna, for sharing the fruits of their stimulating research. All of the talks were both informative and enjoyable. Elizabeth Zacharias, our student representative, organized delightful post-lecture sessions in the Jepson Herbarium where numerous thoughtful and pleasant discussions were held between guest speakers and attendees. Many thanks to Elizabeth for her deft touch in creating such a conducive (and tasty) setting.

This next year promises to be equally exciting if not more so, because this will be the alternating year in which the California Botanical Society's 21st Graduate Student Meeting will be held. The meeting will be held at San Francisco State University's Romberg Tiburon Center for Environmental Studies (Tiburon Center). It will be on Saturday, February 19, 2005. The Tiburon Center is a research and educational facility occupying a spectacular bay view setting on the Tiburon Peninsula in Marin County. There is limited lodging on site and plenty of parking. We will be arranging transportation shuttles for visitors from out of town from the airport to the Tiburon Center. Vicente Garcia, this year's new student representative on the council, Elizabeth Zacharias, last year's student representative, and Diana Benner, a San Francisco State University graduate student, will coordinate the logistical challenges of organizing the meeting. This is an opportunity to showcase the diversity and quality of research that is currently underway by our next generation of botanical scientists. These scientists represent the future of our society and I hope that faculty and members of the society encourage student participation and do everything possible to attend the meeting itself.

On the evening of the Graduate Student Meeting, at the beautiful Tiburon Center Conference Center, we will hold our annual banquet. Our honored guest speaker for the evening will be the distinguished Dr. Arturo Gomez-Pompa. Dr. Gomez-Pompa is a recipient of the 1994 Tyler Prize for Environmental Achievement, member of the National Academies of Science, and distinguished University Professor in the Department of Botany and Plant Sciences at UC Riverside. Dr. Gomez-Pompa has focused on the floristic relationships of economically important tropical plant groups in his native Mexico. He was one of the first scientists to draw the world's attention to our disappearing tropical forests in a classic 1972 paper in *Science*. In a recent paper in *Bioscience* (March 2004), Dr. Gomez-Pompa outlined the challenges facing biodiversity scientists and ethnobotanists and ways that traditional cultural practices of indigenous people might provide solutions to our current biodiversity crisis. Dr. Gomez-Pompa will speak about his latest initiative to promote tropical forest conservation, the Center for Tropical Research (CITRO), a collaborative effort between the University of Vera Cruz and UC Irvine. I am hoping that the banquet is well attended by student participants who may well be excited by the inspiring work that Dr. Gomez-Pompa has accom-

plished, and is still accomplishing, in the arena of biodiversity conservation.

Also, once again, Stefania Mambelli has organized an outstanding public lecture series. Raymond Cranfill of UC Berkeley led off on September 16, 2004, with a talk on "The secret life of ferns"; James Wanket of CSU Sacramento will talk about "Relicts and refugia: late Quaternary forests of the Klamath Mountains" on October 21, 2004. Susan Lambrecht, UC Santa Cruz, will speak on "The cost of flowers in ecological currencies" on November 18, 2004; James Shevock, California Cooperative Ecosystem Studies Unit and council member, will talk about "Bryogeography of California: what can we learn from the mosses about past and future climate changes?" on January 20, 2005; Scott Stephens, UC Berkeley, will review the "Dynamics of the last, intact, Jeffrey pine ecosystem from northwest Mexico: U.S. restoration implications" on March 17, 2005; Elizabeth Wenk, UC Berkeley, will make a presentation on the "Effect of differing substrates on plant physiology and distribution in the alpine Sierra Nevada" on April 21, 2005; and Michelle McMahon, UC Davis, will speak on "Diversification of floral development in the papilionoid legume tribe Amorphaeae" on May 19, 2005. We are all looking forward to this excellent line up of quality presentations.

Everyone who supports the California Botanical Society is helping to keep our public lecture programs, the annual banquet, graduate student research in the botanical sciences, and our journal *Madroño* a vital part of the fabric of our increasing knowledge of the composition and

function of biological diversity in western North America and sister regions to the south. I personally thank all of you for your continued engagement in this effort. I also want to particularly acknowledge the dedication of the editorial staff of *Madroño* and our California Botanical Society council members. Bruce Baldwin continues to make important contributions to the society as past president. Sue Bainbridge, our corresponding secretary, provides invaluable service. It is difficult to imagine the society functioning without her. Staci Markos, our recording secretary, took the lead in getting the Annetta Carter Scholarship Fund off the ground, among her many other important contributions. Roy Buck continues to do fine work in his capacity as the society's treasurer. Jim Shevock provides exemplary work as an at large member, not to mention his monumental work on the mosses of western North America along with Dan Norris in the first two issues of *Madroño* this year. I again thank Elizabeth Zacharias for her wonderful support of the lecture series last year, and we welcome Vicente Garcia and Diana Benner who will work with Elizabeth in organizing this year's Graduate Student Meeting. Also thanks to our web masters, Curtis Clark and John LeDuke. Finally, a farewell thanks to Anne Bradley, former at large member, who served well for much of her term, and welcome to Jeff Corbin who will replace her as a new member of the council. Thanks to all of your collective efforts, we can celebrate an excellent year of accomplishments, and look forward to yet another year of outstanding achievements in 2005.

EDITOR'S REPORT FOR VOLUME 51

This annual report serves to inform the members of the California Botanical Society of the status of *Madroño*, from the number of manuscripts submitted to papers published. Since the previous editor's report (see *Madroño* 50[4]), the journal has received 42 manuscripts for review (30 Articles and 12 Noteworthy Collections); 7 of these Articles have been accepted for publication in that same time period, along with 11 of the Noteworthy Collections. Because we have been getting back on publication schedule over the last year, this period covers only 10 months rather than 12 months as in most previous years. In addition, 20 previously submitted manuscripts were accepted for publication over this period. The average time for article submission to publication remains at approximately six months. Accepted manuscripts are typically published within approximately three to four months. Few manuscripts were rejected after review; authors of *Madroño* articles did a fine job of responding to reviewers' suggestions.

It is amazing to me that this is already my third and final year as Editor. It has been a truly enjoyable and rewarding experience. I'm very happy that we have been able to reach our goal of getting *Madroño* back on schedule. It has been a major challenge over many years and Kristina Schierenbeck deserves much of the credit for her extended tenure as editor prior to my term. On top of our return to a regular publishing schedule, this year marks the largest volume for *Madroño* in the last seven years, thanks in large part to the first two issues on California Mosses by Dan Norris and Jim Shevock. In the future we hope to continue to strengthen the journal and explore new opportunities for publication. If any members have suggestions for special issues of *Madroño* or other ideas for the journal, please let us know.

As always, the publication of *Madroño* involves the efforts of many people, and all of them deserve credit and

thanks for their outstanding contributions. First of all, thanks to the members of the Board of Editors who have provided input on manuscripts and helped to identify important issues for the future of the journal. I especially acknowledge our two outgoing members, David Wood and Ingrid Parker. Similarly, the Executive Council of the California Botanical Society has been incredibly helpful in guiding *Madroño* forward and supporting the journal in every possible way. The long-term dedication of Dieter Wilken (Noteworthy Collections Editor), Margriet Wetherwax (Noteworthy Collections Editor), Jon Keeley (Book Review Editor), and Steve Timbrook (Compiler for Annual Index) has been invaluable for *Madroño*. They deserve enormous thanks for continuing to serve in these important positions. In addition, Laura Wainer, Editorial Assistant, has been very helpful in processing manuscripts and corresponding with authors. Annielaurie Seifert and her colleagues at Allen Press have been extremely helpful and flexible in getting us back on schedule. Thanks to all of these wonderful individuals for their contributions to the journal. In addition, thanks to all of the *Madroño* authors and reviewers who are the heart of the journal. The quality of manuscripts remains high and we look forward to a growing number of submissions in 2005.

Finally, I want to welcome Dr. John Hunter as the new editor of *Madroño*. John will take over with volume 52, and I'm sure he will do an outstanding job in leading the journal forward. New manuscripts can be sent directly to John at the address below, and he can be reached at jhunter@jsanet.com.

Dr. John Hunter
C/O UC Davis Herbarium/Center for Plant Diversity
Plant Biology
One Shields Avenue
University of California Davis
Davis, CA 95616

REVIEWERS OF *MADROÑO* MANUSCRIPTS 2004

Geraldine Allen
Ihsan Al-Shehbaz
Conrad Bahre
Gail Baker
James Bartolome
Bernard Baum
Peter Baye
John Bishop
David Boose
Mark Borchert
Peter Bowler
Thomas Boyle
Marshall Crosby
Taly Drezner
Kate Dwire
Vince Eckhart
Bret Elderd
Erin Espeland
Tracy Feldman
Erica Fleishman

Doug Goldman
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Ted Hogg
Mohammed Kalkhan
Jon Keeley
Ron Lanner
Matt Lavin
Patrick Leary
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Jodi McGraw
John McKay
Steven McLaughlin
Michelle McMahon
Francisco Molina Freaner
James Morefield
J. K. Morton
Rod Myatt
Bob Novak
Bruce Pavlik

Eric Peterson
Diana Pilson
J. Mark Porter
John Sawyer
Kristina Schierenbeck
Paula Schiffman
Rob Schlising
Carl Skinner
Jim Smith
Michael Steele
Mark Stromberg
Arnold Tiehm
Claudia Tyler
Lowell Urbatsch
Robert Utrecho
Tom Van Devender
Jan Van Wagendonk
William Weber
Michael Windham
David Wood

INDEX TO VOLUME 51

Classified entries: major subjects, key words, and results; botanical names (new names are in **boldface**); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

Agavaceae (see *Hesperocallis*)

Agave (see *Hesperocallis*)

Alliaceae (see *Hesperocallis*)

Anacardiaceae (see *Malsoma*)

Apiaceae (see *Cymopterus*)

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DEDICATION



Jean Langenheim

This volume of *Madroño* is dedicated to Jean Langenheim. Jean first arrived in California in 1952 along with her husband, who was a new Assistant Professor of Paleontology at UC Berkeley. She had graduated with Highest Honors from the University of Tulsa in 1946 with a B.S. in Biology, and went on to earn an M.S. in 1949 and a Ph.D. in 1953, under the supervision of the eminent plant ecologist and geobotanist, W. S. Cooper, at the University of Minnesota. The subject of her dissertation was the high mountain vegetation of the Crested Butte, Colorado area. Immediately after completing her Ph.D. she went as a paleobotanist on an expedition to Colombia, thus initiating her Latin American research. She became a Research Associate in the Department of Botany at UC Berkeley in 1954, and Assistant Professor of Biology at San Francisco College for Women in 1956. While at Berkeley she published thought-provoking papers with Herbert Mason, then director of the Herbarium, on semantic analyses of ecological concepts, and also did a study on a Quaternary closed cone pine flora near Little Sur published in *Madroño*. She taught the Field Ecology course at Rocky Mountain Biological Laboratory (RMBL) in 1955 and spent the following summer in Alaska comparing alpine and arctic vegetation. She published her first paper from these Rocky Mountain studies in *Madroño* in 1956. In 1957, along with Bob Ornduff, she assisted Herbert Mason in teaching Field Botany at Sagehen Creek Field Station, where she learned the vegetation of the Sierra Nevada. 1962 found her teaching Field Ecology once again at RMBL, where her successional and vegetation

analyses are still frequently used and a building is named in her honor. Although her research later turned in other directions, she has maintained her interest in and love for high-mountain vegetation throughout her life.

In 1959 she and her husband went to the University of Illinois at Urbana, where she was a Research Associate in the Botany Department, and became a part of their vigorous research activities in both plant ecology and paleobotany. It was here also that she began her research on amber (fossil resin), as part of a UC Berkeley expedition to Chiapas, Mexico. Jean's job on the expedition was to determine the plant source of the resin in which insects had become entrapped. Following this expedition, in 1962 she became a Scholar in the Radcliffe Institute for Independent Study and Research Fellow in the lab of the prominent paleobotanist and geochemist, Elso Barghoorn, at Harvard University. Here she pioneered the use of chemical techniques to determine the plant source of ambers and found convincing evidence for the leguminous genus *Hymenaea* being the source of Chiapas amber. Her subsequent botanical synthesis regarding amber through geologic time ("Amber: a botanical inquiry" in *Science*; 1969) is now considered a classical paper on this subject.

In 1966 she was offered an Assistant Professorship to teach plant ecology at the new UC campus at Santa Cruz. However, before she left Harvard that year she had another experience that influenced the direction of much of her research at UCSC. During her survey of resins through time, she had become fascinated with evolutionary and ecological questions regarding the *raison d'être* of resin

production, which coincided with the beginning of the field of chemical ecology. *Hymenaea* was an ideal model system for a chemical ecological study in an evolutionary framework. However, the center of *Hymenaea*'s distribution was Amazonia and she questioned how she could carry out work there. Serendipitously, a trip with the longtime Amazonian ethnobotanist in Harvard's Botanical Museum, Richard Schultes, enabled her later to initiate at UCSC her long term ecological, systematic and chemical research on *Hymenaea* (and later the related genus *Copaifera*) in Brazilian Amazonia but as well increased her general interest in ethnobotany. The *Hymenaea* and *Copaifera* research expanded throughout the Neotropics and into Africa as well, and has constituted a pioneering coordinated study of resin-producing trees in the tropics.

At UCSC she was the first woman natural scientist and the only one for a number of years as well as the first woman on campus to be promoted to Professor. Despite heavy participation in starting a new campus based on an educational experiment of residential colleges, she has had 40 graduate students at UCSC that she has either sponsored or cosponsored. Some of her students have done dissertations on her projects throughout the New World tropics, and have taken courses in Costa Rica offered by the Organization of Tropical Studies. She had been introduced to OTS in one of the organizations first years in 1963, and she served as the UC representative on the Board of Directors for 15 years, and as VP for Academic Affairs from 1975–1978. Although she had three Brazilian students come to study with her, she also taught chemical ecology in the graduate program at the National Institute for Amazonian Research in Manaus, Brazil in 1974 to assist other Brazilian students to learn more of this emerging field in the tropics. To further help advance research, she chaired the US-Brazil Science Advisory committee for the Humid Tropics (1975–1978) and was a member of the NSF/Brazilian National Research Council Committee on Flora Amazonica (1975–1987). She additionally served as President of the Association for Tropical Biology (1985–1986). Jean was elected to the California Academy of Sciences in 1973.

Jean has studied the chemical ecology of native plants in California and along the Pacific Coast as well as those in agroecosystems. Living on a campus in a redwood forest led her and her students to analyze the variation in the chemistry of the leaf resins of *Sequoia sempervirens* throughout its distribution, and their effects on endophytic fungi and on nitrifying bacteria in the leaf litter. Moreover, fire ecology in the redwood state parks was the subject of a dissertation. Ecological studies of a common understory plant, yerba buena (*Satureja douglasii*), throughout its distribution included effects of abiotic (e.g., light, moisture) and biotic (particularly banana slugs) effects on variation of the essential oils and distribution of the chemotypes. The essential oils of California bay tree (*Umbellularia californica*) also were analyzed for alleopathic effects, including those on nitrifying bacteria, as well as on deter-

rence of deer herbivory. Effects of secondary chemicals from specific intercropped plants on harmful weeds in agro-ecosystems was investigated. Her chemical ecological studies were recognized by her election to the Presidency of the International Society for Chemical Ecology (1986–1987). Jean has recently moved into molecular studies, with one graduate student using DNA analysis to study bacterial communities comprising wetwood in two California species of *Populus* and another the molecular biology of the symbiotic relationship in the prominent California lichen, *Letharia*. Moreover, she has aided California natural history publications by being an editor for the UC Publications in both Botany and Geology as well as a longtime associate editor for *Biochemical Systematics and Ecology*.

Over 130 publications have resulted from her research along with students and collaborators, and her diverse ecological research resulted in her election as President of the Ecological Society of America in (1986–87). A text Botany: *Plant Biology in Relation to Human Affairs* was published in 1982, derived from her popular undergraduate course, "Plants and Human Affairs." She was elected President of the Society for Economic Botany (1993–94). In 2003 she published a comprehensive analysis of resins, *Plant Resin: Chemistry, Ecology, Evolution and Ethnobotany* for which the Society recently gave her their Klinger Award for the best book in ethnobotany for 2004.

Jean's career is a testament to perseverance through much of the period when career options were limited for women. However, her enthusiasm for study of plants, including fossils, has enabled her to pursue a diversity of courses of research, to exert leadership in emerging fields, such as tropical and chemical ecology, and to influence the careers of many students both in field and lecture courses. Her leading the way for women is evident in her having been elected President of four either national or international societies, and having been either the first or second woman president. To recognize the research of other early women ecologists, she has also written several papers on the history of women's accomplishments and contributions to the field.

Although she formally retired in 1993, typically she has continued research by sponsoring or cosponsoring six graduate students since that time as well as published a book. Prophetically, while an undergrad she wrote in a letter to a friend that "I probably will always be a student." Jean has always enjoyed her students not only professionally but also personally, keeping in contact through the years with reunions at meetings and at her home. It is very appropriate that this volume of *Madroño* be dedicated to her.

Thomas S. Hofstra
Sierra Botanical Consulting
22131 Shamrock Lane
Sonora, CA 95370
hofstra@biology.ucsc.edu

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A WEST AMERICAN JOURNAL OF BOTANY

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Editor—DR. JOHN HUNTER
c/o UC Davis Herbarium/Center for Plant Diversity
Plant Biology
One Shields Avenue
University of California Davis
Davis, CA 95616
jhunter@jsanet.com

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HYBRIDIZATION OF *TAMARIX RAMOSISSIMA* AND *T. CHINENSIS*
(SALT CEDARS) WITH *T. APHYLLA* (ATHEL) (TAMARISK) IN THE
SOUTHWESTERN USA DETERMINED FROM DNA
SEQUENCE DATA

JOHN F. GASKIN

U.S. Department of Agriculture, Agricultural Research Service, Northern Plains
Agricultural Research Lab, P.O. Box 463, Sidney, MT 59270
jgaskin@sidney.ars.usda.gov

PATRICK B. SHAFROTH

U.S. Geological Survey, Fort Collins Science Center, 2150 Centre Ave.,
Building C, Ft. Collins, CO 80526

ABSTRACT

Morphological intermediates between *Tamarix ramosissima* or *T. chinensis* (saltcedars) and *T. aphylla* (athel) were found recently in three locations in the southwestern USA, and were assumed to be hybrids or a previously unreported species. We sequenced chloroplast and nuclear DNA from putative parental and hybrid morphotypes and hybrid status of morphological intermediates was supported. Chloroplast data suggest that the seed source for these hybrids is *T. aphylla*. Invasive *T. aphylla* genotypes found in Australia match those found in the USA. Seed was collected from one of the hybrids, and a low percentage of it was viable. This hybrid combination has not been previously reported in the USA or the native ranges of the species. Although populations of this novel *Tamarix* hybrid appear to be uncommon at present, both parental species are considered invasive (saltcedars in North America; athel in Australia), and it is possible that more aggressive hybrid genotypes could be produced. Therefore, natural resource managers concerned with the potential spread of non-native species should be aware of the existence of these plants and monitor their future spread.

Key Words: hybridization, *Tamarix*, tamarisk, saltcedar, athel, invasive.

Accidental and deliberate importations of plants can place historically allopatric species in close proximity (U.S. Congress OTA 1993), which can lead to novel hybridization. These hybrid events may stimulate the evolution of invasiveness in plants (Ellstrand and Schierenbeck 2000) by providing new opportunities for genetic variation and evolutionary novelty (Stebbins 1969) including hybrid traits that exceed those found in the parental types (e.g., Rieseberg et al. 1999). The considerable lag time that can exist between establishment of a naturalized population and its subsequent spread into new areas (often decades or more; Kowarik 1995; Louda et al. 1997), combined with potentially deleterious ecological effects (Vila et al. 2000), emphasizes the need for vigilance over novel hybrids involving naturalized species.

The Old World plant genus *Tamarix* L. (Tamaricaceae) contains about 54 species of shrubs and trees (Baum 1978). Multiple *Tamarix* species were brought to the USA from southern Europe and Asia during the 1800's to be used for shade and erosion control (Baum 1967). The western USA now contains large-scale invasions totaling 470,000–650,000 hectares (Zavaleta 2000) of *T. ramosissima* Ledeb. and *T. chinensis* Lour. (common names “saltcedar” or “tamarisk”). Hybrids of these two species are the most common genotype

in the invasion (Gaskin and Schaal 2002). The two species are morphologically very similar, and hybridization has probably added to their taxonomic confusion.

Another species, *T. aphylla* (L.) H. Karst. (common name “athel”), is native to extreme northern Africa and southwestern Asia (Baum 1978) and has been planted in the USA as a shade and wind break tree but has not spread extensively (Meyers-Rice 1997). In Australia, athel was also imported as a shade tree (perhaps from California in the 1930's (Fuller 1998)), and did not spread for decades until the mid-1970's when large scale invasions occurred, most notably on 400 km of the Finke River in central Australia (Griffin et al. 1989). Oddly, *T. ramosissima* is also naturalized in Australia (Thorpe and Lynch 2000), but unlike *T. aphylla*, has not spread extensively and is not considered a Weed of National Significance. The reason for the historically different behavior of *T. ramosissima* and *T. aphylla* in Australia compared to the USA is unknown, but the recent discovery of thousands of naturalized athels propagated from seed along the shore of Lake Mead, NV (Barnes 2003) suggests that athel has some potential to become invasive in the USA.

Many *Tamarix* species are difficult to distinguish using morphology, especially the saltcedars *T. ra-*

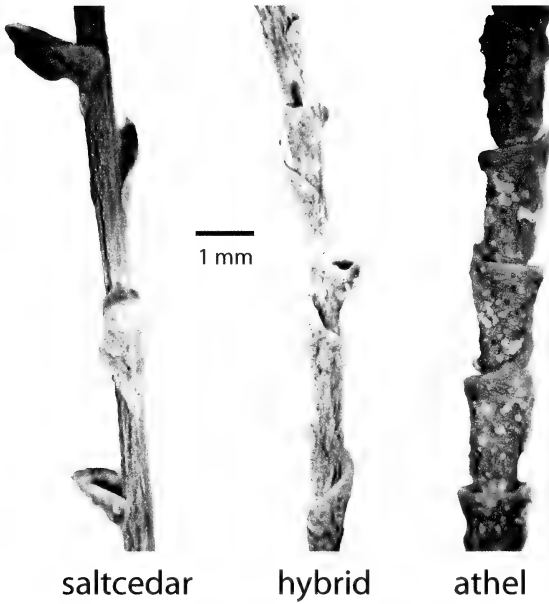


FIG. 1. Leaf morphology of saltcedars (*Tamarix ramosissima* and *T. chinensis*; sessile leaves), athel-saltcedar hybrid (strongly clasping leaves), and athel (*T. aphylla*; vaginate leaves).

mosissima and *T. chinensis* (Crins 1989; Gaskin and Schaal 2003). However, *T. aphylla* is very distinct from *T. ramosissima* and *T. chinensis* due to its vaginate (completely sheathing the stem) instead of sessile leaves (Fig. 1) and its tree habit under favorable conditions, compared to a large shrub habit. The floral morphology within the genus *Tamarix* can vary from 4–5 sepals, 4–5 petals, and

4–15 stamens, but *T. aphylla*, *T. ramosissima* and *T. chinensis* are extremely similar, each with a pentamerous calyx, corolla, and androecium (Baum 1978).

Within the last few years three populations have been found in the southwestern USA containing leaf morphologies that are intermediate to *T. ramosissima* or *T. chinensis* (hereafter referred to as saltcedars) and *T. aphylla* (hereafter referred to as athel), suggesting that they may be a novel hybrid, or a species of *Tamarix* previously unreported in the USA. Here, we genetically characterize the morphologically intermediate plants from the three populations using chloroplast and nuclear DNA sequence markers to determine their identity. We also genetically compare invasive specimens of athel from Australia with newly invasive athel specimens from the USA.

METHODS

Study Areas

The populations that are morphologically intermediate to athel and saltcedar are known from only three locations (Fig. 2). One is within a stand dominated by athel on Boulder Beach, Lake Mead, NV (ca. 36°2'46"N lat., 114°48'24"W long., elev. 370 m). The area also contains numerous saltcedars closer to the lake edge. The number of intermediates present at Boulder Beach is unknown, but we found five in an informal survey of a small portion (ca. 1.0 ha) of the athel stand.

The second area containing morphologically intermediate plants is near Walter's Camp along the Colorado River, ca. 40 km south of Blythe, CA (ca. 33°15'9"N lat., 114°41'48"W long., elev. 63 m).

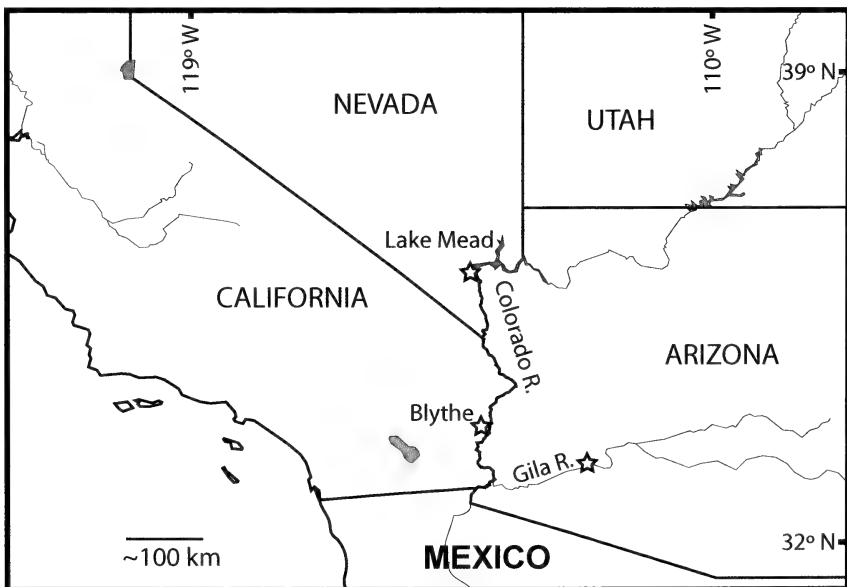


FIG. 2. Locations of *Tamarix* populations containing hybrids between athel and saltcedar (indicated by stars).

TABLE 1. MORPHOLOGICAL AND GENOTYPIC DESCRIPTION OF VOUCHERS USED IN STUDY OF HYBRIDIZATION OF *TAMARIX RAMOSISSIMA* AND *T. CHINENSIS* (SALT CEDAR) AND *T. APHYLLA* (ATHEL).

| Plant DNA # | Leaf morphology | <i>trn</i> G-S chloroplast genotype | Chloroplast genotype similar to: | <i>pepC</i> nuclear genotype | Nuclear genotype similar to: | Voucher # | Location |
|-------------|-----------------|-------------------------------------|----------------------------------|------------------------------|------------------------------|--------------------|-------------|
| USA | | | | | | | |
| 3111 | saltcedar | A | saltcedar | 1/1 | saltcedar | <i>Gaskin 3111</i> | Gila River |
| 3119 | saltcedar | D | ? | 1/1 | saltcedar | <i>Gaskin 3119</i> | Gila River |
| 3122 | saltcedar | Q | athel | 2/2 | saltcedar | <i>Gaskin 3122</i> | Gila River |
| 4103 | saltcedar | G | saltcedar | 12/50 | saltcedar/? | <i>Barnes s.n.</i> | Lake Mead |
| 4105 | saltcedar | A | saltcedar | 1/50 | saltcedar/? | <i>Barnes s.n.</i> | Lake Mead |
| 4108 | saltcedar | A | saltcedar | 1/2 | saltcedar | <i>Barnes s.n.</i> | Lake Mead |
| 3121 | athel | Q | athel | 61/62 | athel | <i>Gaskin 3121</i> | Gila River |
| 4100 | athel | Q | athel | 61/61 | athel | <i>Barnes s.n.</i> | Lake Mead |
| 4102 | athel | Q | athel | 61/61 | athel | <i>Barnes s.n.</i> | Lake Mead |
| 4104 | athel | Q | athel | 61/61 | athel | <i>Barnes s.n.</i> | Lake Mead |
| 4098 | intermediate | Q | athel | 2/59 | hybrid | <i>Barnes s.n.</i> | Lake Mead |
| 4101 | intermediate | Q | athel | 2/62 | hybrid | <i>Barnes s.n.</i> | Lake Mead |
| 4106 | intermediate | Q | athel | 2/62 | hybrid | <i>Barnes s.n.</i> | Lake Mead |
| 4107 | intermediate | Q | athel | 2/62 | hybrid | <i>Barnes s.n.</i> | Lake Mead |
| 3113 | intermediate | Q | athel | 60/63 | hybrid | <i>Gaskin 3113</i> | Gila River |
| 3116 | intermediate | Q | athel | 1/62 | hybrid | <i>Gaskin 3116</i> | Gila River |
| 3120 | intermediate | Q | athel | 1/62 | hybrid | <i>Gaskin 3120</i> | Gila River |
| 4494 | intermediate | Q | athel | 2/62 | hybrid | <i>Shafroth B1</i> | Blythe |
| 4495 | intermediate | Q | athel | 1/62 | hybrid | <i>Shafroth B2</i> | Blythe |
| 4496 | intermediate | Q | athel | 2/65 | hybrid | <i>Shafroth B3</i> | Blythe |
| 4497 | intermediate | Q | athel | 2/65 | hybrid | <i>Shafroth B4</i> | Blythe |
| 4498 | intermediate | Q | athel | 2/65 | hybrid | <i>Shafroth B5</i> | Blythe |
| 4499 | intermediate | Q | athel | 2/62 | hybrid | <i>Shafroth B6</i> | Blythe |
| 4500 | intermediate | Q | athel | 2/65 | hybrid | <i>Shafroth B7</i> | Blythe |
| Australia | | | | | | | |
| 2043 | athel | Q | athel | 61/62 | athel | <i>Gavin 2</i> | Finke River |
| 2044 | athel | Q | athel | 61/61 | athel | <i>Gavin 3</i> | Finke River |
| 2045 | athel | Q | athel | 61/61 | athel | <i>Gavin 4</i> | Finke River |
| 2046 | athel | Q | athel | 61/61 | athel | <i>Gavin 5</i> | Finke River |
| 2047 | athel | Q | athel | 61/62 | athel | <i>Gavin 6</i> | Finke River |
| 2048 | athel | Q | athel | 60/61 | athel | <i>Gavin 7</i> | Finke River |

There were eight intermediates within a ca. 0.05 ha area at the upland-bottomland interface, adjacent to saltcedars. There are hundreds of athels planted at abandoned settlements within about 5 km of this site, and at least one other intermediate was observed ca. 2.5 km from the group of eight intermediates from which we collected samples, less than 100 m from a large population of saltcedars.

The third population is over 400 km from the Lake Mead site and over 160 km from the Blythe site, along the Gila River approximately 4 km downstream of Painted Rock dam in Maricopa County, AZ (ca. 33°5'2"N lat., 113°3'19"W long., elev. 160 m). The morphologically intermediate plants are located near athels that were most likely planted as a wind break in an agricultural setting near the mouth of an ephemeral wash, and numerous saltcedars are found nearby. *Tamarix* plants within three vegetation patches that contained at least some of the morphologically intermediate plants were censused. The area of the patches to-

taled 2.1 hectares, and a total of 139 athels, 134 saltcedars, and 28 intermediates were counted. Other nearby patches of saltcedar did not appear to contain intermediates; however, our survey was not comprehensive. Age estimates of the intermediates range from 8–13 years based on counts of annual rings on stem cross-sections cut from the main stem (below surface branch points) of six individuals.

Australian athel samples were provided from Horseshoe Bend on the Finke River, Northern Territory (six separate sites, ca. 25°13'S lat., 134°11'E long.). Representative vouchers, listed in Table 1, have been deposited at the Missouri Botanical Garden herbarium (MO).

Morphology

Identity of specimens was determined using the key to species in Baum (1978) which covers the genus worldwide. Morphological intermediacy was determined from leaf morphology alone because

very few plants were fertile at the time of collection.

Tissue Sampling

Leaf tissue samples were collected from 24 *Tamarix* individuals from the three USA sites. Of these, six have sessile leaves typical of saltcedar (e.g., *T. ramosissima* or *T. chinensis*), four have vaginate leaves typical of athel (*T. aphylla*), and 14 have morphologically intermediate leaves that strongly clasp the stem, but are not completely vaginate. Leaf tissue was also taken from the six Australian athel samples.

DNA Isolation, PCR Amplification and Sequencing

Fresh, silica dried tissue was used for DNA extraction. Genomic DNA was isolated using a modified CTAB method (Hillis et al. 1996). PCR amplification of the chloroplast intergenic region between the *trn S* (GCU) and *trn G* (UCC) genes utilized the primer pair *trn S* (GCU) (5'-GCCGCTTTAGTCCACTCAGC-3') and *trn G* (UCC) (5'-GAACGAATCACACTTTTACCAC-3') of Hamilton (1999) with the following cycling conditions: 95°C (2 min); 30 cycles of 95°C (1 min), 55°C (1min), 72°C (2 min); and then 32°C (5 min). The nuclear fourth *pepC* (phosphoenolpyruvate carboxylase) intron region was amplified by PCR using primer pair PPCL1 (forward) (5'-GTCCCTAAGTTTCTGCGTCG-3') and PPCL2 (reverse) (5'-CTTCAGGTGTTACTCTTGGG-3') (designed by J.G.) with the following cycling conditions: 95°C (2 min); 30 cycles of 95°C (1 min), 50°C (1 min), 72°C (2 min); and then 32°C (5 min). A 50-μl reaction was performed for each individual, and PCR products were purified using QIAquick PCR Purification kit (Qiagen, Valencia, CA). Purified templates were sequenced in two directions by using either an ABI 373A or a Beckman CEQ 2000XL automated sequencer, using the same primers listed above. Sequences generated in this study are available on GenBank, and accession numbers are listed in Table 2. For heterozygous nuclear sequences, haplotypes were first inferred using "haplotype subtraction" (Clark 1990). To verify our estimation of nuclear haplotypes not found in the homozygotic states, we sequenced cloned PCR products of selected heterozygotic plants. Cloning was done on purified template with TOPO TA Cloning Kit for Sequencing (Invitrogen, Carlsbad, CA) using standard protocol for chemically competent cells. Cell cultures were grown on kanamycin plates, and individual colonies were picked from the plates, amplified, purified, and then sequenced using the protocols listed above. Haplotype sequences were manually aligned using the software Se-Al (Rambaut 1996). The alignment is available upon request from the first author. Most parsimonious haplotype networks were created by hand. Insertion/deletion

TABLE 2. GENBANK ACCESSION NUMBERS FOR *TAMARIX* HAPLOTYPES.

| | |
|------------------------|----------|
| Nuclear haplotypes | |
| 1 | AY090385 |
| 2 | AY090386 |
| 12 | AY090396 |
| 50 | AY090434 |
| 59 | AY672672 |
| 60 | AY672673 |
| 61 | AY672671 |
| 62 | AY672674 |
| 63 | AY672675 |
| 65 | AY672676 |
| Chloroplast haplotypes | |
| A | AF490798 |
| D | AF539998 |
| Q | AF490795 |
| G | AF490782 |

events, no matter what size, were treated as one mutational event (one evolutionary step).

Testing Seed Viability

Seeds were plated between discs of filter paper in a standard Petri dish, and moistened with distilled H₂O. Petri dishes were subjected to 24°C and 14 hrs of light per day. After 48 hours, seeds that turned green and had a root radicle emerge from the seed coat were considered viable.

RESULTS

Morphology

We attempted to use the species key (Baum 1978) for the few plants with intermediate leaf morphology that were fertile, but failed to identify them to species with this method. Their leaf morphology most closely resembled *T. bengalensis* Baum or *T. indica* Willd. The morphological intermediates differ from *T. bengalensis* in having conspicuous salt glands and 1 mm narrowly ovate sepals rather than 1.25–1.5 mm orbicular to broadly ovate sepals, and they differ from *T. indica* in having entire sepals rather than deeply incised-denticulate sepals, especially towards the sepal apex. The 1.75 mm obovate petals of the few fertile intermediates most closely resemble those of *T. ramosissima*.

Chloroplast Marker

The *trn S* (GCU)–*trn G* (UCC) intergenic region sequenced is 1001 bases in length. The plants that morphologically resemble saltcedar have chloroplast haplotypes A, D, G, or Q. In a previous study (Gaskin 2003) haplotype A was found in 77% (n = 23) of USA saltcedars, D was found in 3% (n = 1) (but this haplotype is most often found in *T. parviflora* DC. in the USA (Gaskin and Schaal 2003)), and G was found in 17% (n = 5) (usually found in the horticultural *T. ramosissima* 'Pink

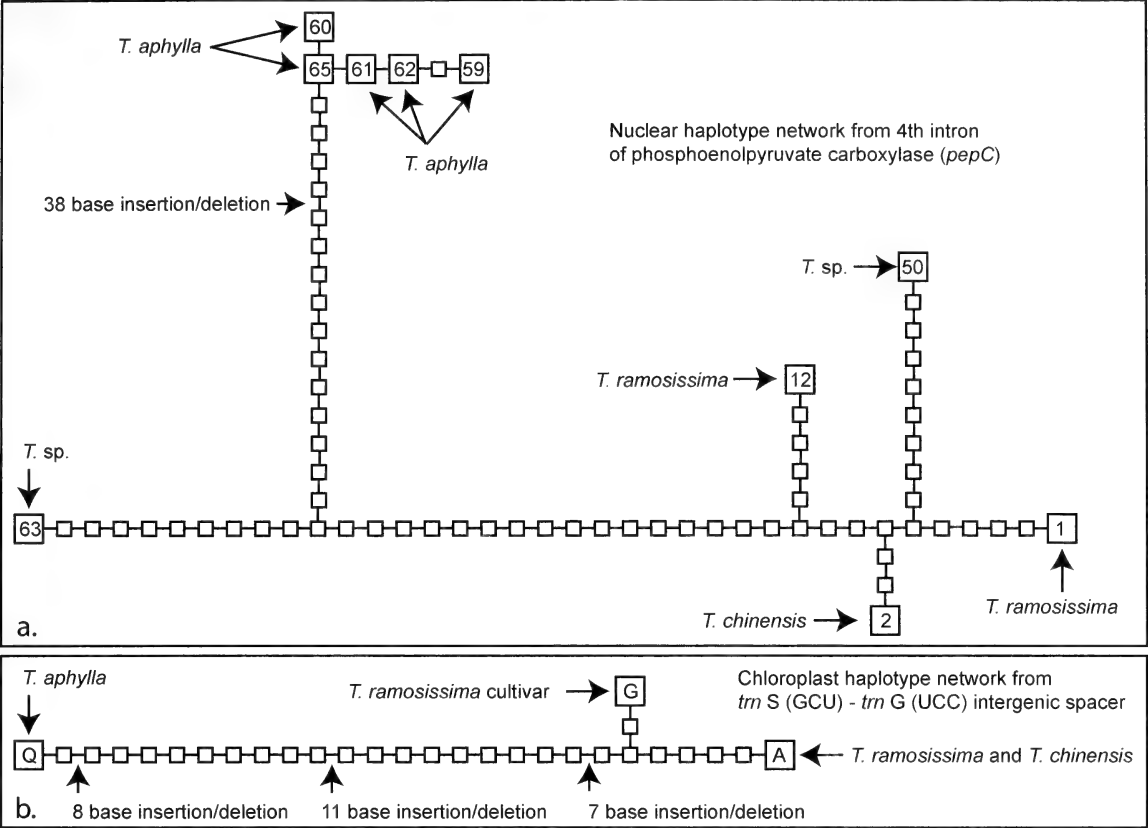


FIG. 3. Haplotype networks (gene genealogies) of the nuclear phosphoenolpyruvate carboxylase (*pepC*) 4th intron region (a) and chloroplast *trn S* (GCU)–*trn G* (UCC) intergenic region (b). Boxes with numbers or letters represent haplotypes (alleles) recovered. The smaller empty boxes represent intermediate haplotypes not recovered in this analysis. Lines separating boxes represent a single point mutation or insertion/deletion event.

Cascade’ cultivar (Gaskin 2003)). Athel samples from the USA and Australia all contain the haplotype Q, which is 26 (2.6%) mutational differences (including 7, 8, and 11 base insertion/deletions) from the saltcedar haplotype A (Fig. 3). The samples with intermediate morphologies all contain haplotype Q, which is also found in all athel in this study. Chloroplast haplotype names follow Gaskin (2003).

Nuclear Marker

The *pepC* intron region sequenced is approximately 900 bases in length. Initial direct sequencing of PCR product found 13 genotypic combinations (see Table 3), three of which are homozygotic (1/1, 2/2, and 61/61). From the direct sequencing data we infer that there are ten haplotypes (1, 2, 12, 50, 59, 60, 61, 62, 63, and 65). The existence of haplotypes 1, 2, and 61 are obvious from their presence in homozygotic plants. To verify the sequences of other inferred haplotypes found only in heterozygotes, we sequenced cloned product from specimens 3113 (genotype 60/63), 3121 (61/62), 4098 (2/59), 4103 (12/50), 4105 (1/50), 4106 (2/62),

4108 (1/2), and 4500 (2/65). In each case the cloned product sequences exactly matched one of the inferred haplotypes from that plant.

The plants that morphologically resemble saltcedar contain nuclear genotypes 1/1, 2/2, 1/2, 1/50, and 12/50. The first four genotypes are identical to those found in 21% (n = 32), 19% (n = 30), 21% (n = 33), and 1% (n = 2) (respectively) of the USA saltcedars sampled in a previous study (Gaskin and Schaal 2002). Genotype 12/50 was not found in that study, but is composed of two haplotypes that were found in 10% and 1% (respectively) of the USA saltcedars (Gaskin and Schaal 2002). Nuclear haplotypes designations follow Gaskin and Schaal (2002).

The USA athel specimens have genotypes 60/61, 61/61, and 61/62, and the haplotypes involved in these genotypic combinations cluster tightly on the gene tree (Fig. 3), differing by only three mutations, and are at least 39 (4.3%) mutational differences (including a prominent 38 base insertion/deletion) away from haplotypes found in plants that morphologically resemble the saltcedars (1, 2, 12, and 50). The Australian athel samples have genotypes 60/

TABLE 3. NUCLEOTIDE STATE AT VARIABLE LOCI OF THE NUCLEAR FOURTH *PEPC* (PHOSPHOENOLPYRUVATE CARBOXYLASE) INTRON REGION OF *TAMARIX* SPP.

| Leaf morphology | Nuclear geno-type | Nucleotide site # | | | | | | | | | | | | |
|-----------------|-------------------|-------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | | 1 | 13 | 108 | 109 | 112 | 150 | 152 | 162 | 189 | 191 | 197 | 245 | 264 |
| Saltcedar | 1/1 | G | T | T | G | A | A | A | A | T | T | T | C | A |
| Saltcedar | 1/2 | G | T | T | G | A | A | A | A | T | T | T | C | A |
| Saltcedar | 1/50 | G | T | T | G | A | A | A | A | T | T | C/T | C | A |
| Saltcedar | 2/2 | G | T | T | G | A | A | A | A | T | T | T | C | A |
| Saltcedar | 12/50 | G | T | T | G | A | A | A | A | T | T | C/T | C | A |
| Intermediate | 1/62 | A/G | C/T | C/T | C/G | A/C | A/C | A/G | A/C | T | T | T | C/G | A/C |
| Intermediate | 2/59 | A/G | C/T | C/T | C/G | A/C | A/C | A/G | A/C | A/T | A/T | T | C/G | A/C |
| Intermediate | 2/62 | A/G | C/T | C/T | C/G | A/C | A/C | A/G | A/C | T | T | T | C/G | A/C |
| Intermediate | 2/65 | A/G | C/T | C/T | C/G | A/C | A/C | A/G | A/C | T | T | T | C/G | A/C |
| Intermediate | 60/63 | A | C | C/T | C | C | C | A/G | A/C | T | T | T | G | C |
| Athel | 60/61 | A | C | C | C | C | C | G | C | T | T | T | G | C |
| Athel | 61/61 | A | C | C | C | C | C | G | C | T | T | T | G | C |
| Athel | 61/62 | A | C | C | C | C | C | G | C | T | T | T | G | C |

| Leaf morphology | Nuclear geno-type | Nucleotide site # | | | | | | | | | | | | |
|-----------------|-------------------|-------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | | 266 | 277 | 289 | 297 | 300 | 343 | 359 | 397 | 400 | 410 | 431 | 450 | 453 |
| Saltcedar | 1/1 | A | A | A | G | G | C | C | A | C | A | T | T | T |
| Saltcedar | 1/2 | A/T | A/G | A | G | G | C | C | A | C | A/T | A/T | T | T |
| Saltcedar | 1/50 | A | G | A | G | G | C | C | A | C | A | A/T | A | A/T |
| Saltcedar | 2/2 | T | G | A | G | G | C | C | A | C | T | A | — | T |
| Saltcedar | 12/50 | A | G | A | G | A/G | C | C | A | C | A | A | A | A/T |
| Intermediate | 1/62 | A | A/G | A/C | G/T | A/G | C/T | C/T | A/C | C/T | A/C | A/T | T | T |
| Intermediate | 2/59 | T | G | A/C | G/T | A/G | C/T | C/T | A/C | C/T | T | A | — | T |
| Intermediate | 2/62 | T | G | A/C | G/T | A/G | C/T | C/T | A/C | C/T | T | A | — | T |
| Intermediate | 2/65 | T | G | A/C | G/T | A/G | C/T | C/T | A/C | C/T | T | A | — | T |
| Intermediate | 60/63 | A | G | C | T | A | C/T | T | C | C/T | A/C | A | A/T | T |
| Athel | 60/61 | A | G | C | T | A | T | T | C | T | C | A | T | T |
| Athel | 61/61 | A | G | C | T | A | T | T | C | T | C | A | T | T |
| Athel | 61/62 | A | G | C | T | A | T | T | C | T | C | A | T | T |

| Leaf morphology | Nuclear geno-type | Nucleotide site # | | | | | | | | | | | | |
|-----------------|-------------------|-------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | | 455 | 460 | 466 | 496 | 498 | 503 | 514 | 554 | 555 | 568 | 574 | 576 | 587 |
| Saltcedar | 1/1 | T | A | T | T | G | A | C | T | A | A | C | C | C |
| Saltcedar | 1/2 | T | A | T | C/T | A/G | A | C | T | A | A/G | C | C | C |
| Saltcedar | 1/50 | A/T | A | T | C/T | A/G | A/T | C | T | A | A | C | C | C |
| Saltcedar | 2/2 | T | A | T | C | A | A | C | T | A | G | C | C | C |
| Saltcedar | 12/50 | A/T | A | G/T | C/T | A | A/T | C | T | A | A | C | C | C |
| Intermediate | 1/62 | T | A | T | T | A/G | A | C/G | C/T | A/G | A | C/T | C | C/T |
| Intermediate | 2/59 | T | A | T | C | A | A | C/G | C/T | A/G | A | C/T | C | C/T |
| Intermediate | 2/62 | T | A | T | C | A | A | C/G | C/T | A/G | A | C/T | C | C/T |
| Intermediate | 2/65 | T | A | T | C | A | A | C/G | C/T | A/G | A | C/T | C | C/T |
| Intermediate | 60/63 | T | A/G | T | T | A | A | G | C/T | A/G | A | C/T | A/C | T |
| Athel | 60/61 | T | A | T | T | A | A | G | C | G | A | T | C | T |
| Athel | 61/61 | T | A | T | T | A | A | G | C | G | A | T | C | T |
| Athel | 61/62 | T | A | T | T | A | A | G | C | G | A | T | C | T |

61, 61/61, and 61/62, which are all identical to athel genotypes found in the USA.

The samples with intermediate morphologies all have heterozygous genotypes for this diploid marker. Some haplotypes found in these heterozygotes (1, 2, 60, and 62) match exactly those found in the athel and saltcedar specimens, while haplotypes 59, 63, and 65 do not. Haplotypes 59 and 65 are most likely athel haplotypes, as they are very close (one

mutation) to the cluster of athels on the gene tree. The taxonomic origin of haplotype 63 is unknown, as it is distant from all other haplotypes and taxa in this study. The morphologically intermediate genotypes are 1/62 (*T. ramosissima* × *T. aphylla*), 2/62 (*T. chinensis* × *T. aphylla*), 2/59 (*T. chinensis* × *T. aphylla*?), 2/65 (*T. chinensis* × *T. aphylla*?), and 63/60 (*T. sp.* × *T. aphylla*). None of the genotypes found in morphologically intermediate

TABLE 3. CONTINUED.

| Leaf morphology | Nuclear geno-type | Nucleotide site # | | | | | | | | | | | | |
|-----------------|-------------------|-------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | | 588 | 610 | 615 | 628 | 636 | 637 | 686 | 696 | 697 | 710 | 711 | 712 | 713 |
| Saltcedar | 1/1 | A | T | | A | C | G | G | T | G | C | T | G | A |
| Saltcedar | 1/2 | A | T | T | A | C | G | G | T | G | C | T | G | A |
| Saltcedar | 1/50 | A | T | T | A/- | C/T | G | G | T | G | C | T | G | A |
| Saltcedar | 2/2 | A | T | T | A | C | G | G | T | G | C | T | G | A |
| Saltcedar | 12/50 | A | T | T | A/- | C/T | G | G | T | G | C | T | G | A |
| Intermediate | 1/62 | A/G | C/T | T | A | C | G | A/G | T | G/T | C/- | T/- | G/- | A/- |
| Intermediate | 2/59 | A/G | C/T | T | A | C | G | A/G | T | G/T | C/- | T/- | G/- | A/- |
| Intermediate | 2/62 | A/G | C/T | T | A | C | G | A/G | T | G/T | C/- | T/- | G/- | A/- |
| Intermediate | 2/65 | A/G | C/T | T | A | C | G | A/G | T | G/T | C/- | T/- | G/- | A/- |
| Intermediate | 60/63 | G | C/T | C/T | A | C | A/G | A | C/T | G/T | C/- | T/- | G/- | A/- |
| Athel | 60/61 | G | C | T | A | C | G | A | T | T | — | — | — | — |
| Athel | 61/61 | G | C | T | A | C | G | A | T | T | — | — | — | — |
| Athel | 61/62 | G | C | T | A | C | G | A | T | T | — | — | — | — |

| Leaf morphology | Nuclear geno-type | Nucleotide site # | | | | | | | | | | | | |
|-----------------|-------------------|-------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | | 714 | 715 | 716 | 717 | 718 | 719 | 720 | 721 | 722 | 723 | 724 | 725 | 726 |
| Saltcedar | 1/1 | A | G | C | T | G | A | T | A | T | G | T | T | G |
| Saltcedar | 1/2 | A | G | C | T | G | A | T | A | T | G | T | T | G |
| Saltcedar | 1/50 | A | G | C | T | G | A | T | A | T | G | T | T | G |
| Saltcedar | 2/2 | A | G | C | T | G | A | T | A | T | G | T | T | G |
| Saltcedar | 12/50 | A | G | C | T | G | A | T | A | T | G | T | T | G |
| Intermediate | 1/62 | A/- | G/- | C/- | T/- | G/- | A/- | T/- | A/- | T/- | G/- | T/- | T/- | G/- |
| Intermediate | 2/59 | A/- | G/- | C/- | T/- | G/- | A/- | T/- | A/- | T/- | G/- | T/- | T/- | G/- |
| Intermediate | 2/62 | A/- | G/- | C/- | T/- | G/- | A/- | T/- | A/- | T/- | G/- | T/- | T/- | G/- |
| Intermediate | 2/65 | A/- | G/- | C/- | T/- | G/- | A/- | T/- | A/- | T/- | G/- | T/- | T/- | G/- |
| Intermediate | 60/63 | A/- | G/- | C/- | T/- | G/- | A/- | T/- | A/- | T/- | G/- | T/- | T/- | G/- |
| Athel | 60/61 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Athel | 61/61 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Athel | 61/62 | — | — | — | — | — | — | — | — | — | — | — | — | — |

| Leaf morphology | Nuclear geno-type | Nucleotide site # | | | | | | | | | | | | |
|-----------------|-------------------|-------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | | 727 | 728 | 729 | 730 | 731 | 732 | 733 | 734 | 735 | 736 | 737 | 738 | 739 |
| Saltcedar | 1/1 | T | G | G | C | T | T | T | T | A | A | T | A | T |
| Saltcedar | 1/2 | T | G | G | C | T | T | T | T | A | A | T | A | T |
| Saltcedar | 1/50 | T | G | G | C | T | T | T | T | A | A | T | A | T |
| Saltcedar | 2/2 | T | G | G | C | T | T | T | T | A | A | T | A | T |
| Saltcedar | 12/50 | T | G | G | C | T | T | T | T | A | A | T | A | T |
| Intermediate | 1/62 | T/- | G/- | G/- | C/- | T/- | T/- | T/- | T/- | A/- | A/- | T/- | A/- | T/- |
| Intermediate | 2/59 | T/- | G/- | G/- | C/- | T/- | T/- | T/- | T/- | A/- | A/- | T/- | A/- | T/- |
| Intermediate | 2/62 | T/- | G/- | G/- | C/- | T/- | T/- | T/- | T/- | A/- | A/- | T/- | A/- | T/- |
| Intermediate | 2/65 | T/- | G/- | G/- | C/- | T/- | T/- | T/- | T/- | A/- | A/- | T/- | A/- | T/- |
| Intermediate | 60/63 | T/- | G/- | G/- | C/- | T/- | T/- | T/- | T/- | A/- | A/- | T/- | A/- | T/- |
| Athel | 60/61 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Athel | 61/61 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Athel | 61/62 | — | — | — | — | — | — | — | — | — | — | — | — | — |

plants were ever detected in a previous analysis of 269 saltcedars worldwide (Gaskin and Schaal 2002).

Viability of Seed with Intermediate Morphology

One plant (*Shafroth B1*) from near Walters Camp, CA was in seed on December 12, 2003. Seeds were plated three days after being collected, and nine of the 239 seeds (3.8%) exhibited viability.

DISCUSSION

The nuclear genotypes found in the morphologically intermediate plants are most often exact combinations of athel and saltcedar haplotypes, supporting our first hypothesis of hybridization. The presence of chloroplast sequence in the morphologically intermediate plants that is identical to that found in all specimens of athel also supports the hypothesis of hybridization. The DNA data do not support the hypothesis of morphologically inter-

TABLE 3. CONTINUED.

| Leaf morphology | Nuclear geno-type | Nucleotide site # | | | | | | | | | | | | |
|-----------------|-------------------|-------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | | 740 | 741 | 742 | 743 | 744 | 745 | 746 | 747 | 778 | 782 | 797 | 798 | 821 |
| Saltcedar | 1/1 | T | G | T | A | T | A | C | T | G | A | G | G | T |
| Saltcedar | 1/2 | T | G | T | A | T | A | C | T | G | A | G | G | T |
| Saltcedar | 1/50 | T | G | T | A | T | A | C | T | G | A | G | G | T |
| Saltcedar | 2/2 | T | G | T | A | T | A | C | T | G | A | G | G | T |
| Saltcedar | 12/50 | T | G | C/T | A | T | A | C | T | G | A | C/G | G | T |
| Intermediate | 1/62 | T/- | G/- | T/- | A/- | T/- | A/- | C/- | T/- | A/G | A | C/G | A/G | C/T |
| Intermediate | 2/59 | T/- | G/- | T/- | A/- | T/- | A/- | C/- | T/- | A/G | A | C/G | A/G | C/T |
| Intermediate | 2/62 | T/- | G/- | T/- | A/- | T/- | A/- | C/- | T/- | A/G | A | C/G | A/G | C/T |
| Intermediate | 2/65 | T/- | G/- | T/- | A/- | T/- | A/- | C/- | T/- | A/G | A | C/G | A/G | C/T |
| Intermediate | 60/63 | T/- | G/- | T/- | A/- | T/- | A/- | C/- | T/- | A/G | A/G | C | A/G | C |
| Athel | 60/61 | — | — | — | — | — | — | — | — | A | A | C | A | C |
| Athel | 61/61 | — | — | — | — | — | — | — | — | A | A | C | A | C |
| Athel | 61/62 | — | — | — | — | — | — | — | — | A | A | C | A | C |

| Leaf morphology | Nuclear geno-type | Nucleotide site # | | | | | | | | | | | |
|-----------------|-------------------|-------------------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| | | 825 | 847 | 863 | 890 | 891 | 892 | 893 | 894 | 895 | 902 | 905 | 906 |
| Saltcedar | 1/1 | G | G | G | — | — | — | — | — | — | A | C | A |
| Saltcedar | 1/2 | G | G | G | — | — | — | — | — | — | A | C | A/G |
| Saltcedar | 1/50 | G | G/T | G | — | — | — | — | — | — | A | C | A |
| Saltcedar | 2/2 | G | G | G | — | — | — | — | — | — | A | C | G |
| Saltcedar | 12/50 | G | G/T | G | — | — | — | — | — | — | A | C/T | A/G |
| Intermediate | 1/62 | G/T | G | A/G | — | — | — | — | — | — | A | C/T | A/G |
| Intermediate | 2/59 | G/T | G | A/G | — | — | — | — | — | — | A | C/T | G |
| Intermediate | 2/62 | G/T | G | A/G | — | — | — | — | — | — | A | C/T | G |
| Intermediate | 2/65 | G/T | G | A/G | — | — | — | — | — | — | A/G | C | G |
| Intermediate | 60/63 | T | G | A | A/- | T/- | A/- | T/- | G/- | A/- | G | C/T | A/G |
| Athel | 60/61 | T | G | A | — | — | — | — | — | — | A/G | C/T | G |
| Athel | 61/61 | T | G | A | — | — | — | — | — | — | A | C | G |
| Athel | 61/62 | T | G | A | — | — | — | — | — | — | A | C/T | G |

mediate plants being a previously unrecorded species in the USA, as none of the morphologically intermediate plants contain chloroplast sequences different from those found commonly in other *Tamarix* species in the USA, and all morphologically intermediate plants contain at least one nuclear haplotype commonly found in a putative parental species. The seed source of the hybrid plants investigated is athel, assuming maternal inheritance of the chloroplast marker. Most angiosperms exhibit this inheritance pattern (Reboud and Zeyl 1994), however, cpDNA can occasionally be inherited from either parent or biparentally, as in *Turnera* L. (Shore and Triassi 1998). Plastid inheritance in the family Tamaricaceae has not been investigated.

The three different Australian athel nuclear marker genotypes are identical to athel genotypes found in the USA. Perhaps with a more variable marker, Australian specimens could be distinguished from USA specimens, but at this point, given the genetic similarity and the observations of seedling establishment on Lake Mead (Barnes 2003), we should assume that the athel present in the USA, under certain conditions, could invade more sites. However, athel has been present for sev-

eral decades in the western USA at a variety of sites and has not yet spread extensively.

The saltcedar *Tamarix chinensis* (represented by nuclear haplotype 2) and athel are allopatric in Eurasia, with haplotype 2 native to eastern China (Gaskin and Schaal 2002) and athel ranging from northern Africa to Pakistan (Baum 1978). Thus, we expect that the hybrids between these two historically allopatric species are novel. The ranges of the saltcedar *T. ramosissima* and athel overlap slightly in areas of Asia, but hybrids of athel and saltcedar are not mentioned in the Eurasian literature, nor did the authors note them while collecting in areas of Asia where the two species are sympatric.

There is genetic variation within the hybrids, indicated by the five different nuclear genotypes found in our small sample of 14 plants of intermediate morphology. Crosses between hybrids or backcrosses with either parent could increase the number of genotypes, providing additional evolutionary opportunities for the success of the hybrid lineage. One of the plants (*Gaskin 3122*), classified as saltcedar according to its morphology and nuclear genotype (Q). The sample was re-sequenced to con-

firm this result. The presence of the athel chloroplast haplotype Q in this plant must have occurred through backcrossing of a hybrid with a saltcedar or another hybrid plant (e.g., crossing Q-60/60 with A-2/2, resulting in the hybrid Q-60/2, then backcrossing the hybrid with a saltcedar A-2/2, resulting in a plant with chloroplast-nuclear genotype Q-2/2).

Our observed 3.8% viability of seed from one of the hybrids is low compared to up to 98% viability for *T. ramosissima* and 100% viability for *T. aphylla* when germinated with tap water within a week after collection (Horton 1960; Waisel 1960). However, we do not know how long our seeds had been mature and attached to the plant before being collected. Seed viability of both species is known to decrease with storage time after collection (Horton 1960; Waisel 1960), and saltcedar seed viability can decrease to as low as 20% after 10 weeks under field conditions (Horton 1960).

Even with a low viability rate, a hybrid could still produce a substantial number of viable seeds, as mature saltcedars have been estimated to produce several hundred thousand seeds in a single growing season (Merkel 1957). However, besides the molecular evidence of backcrossing and the one plant producing seed near Walters Camp, CA, we found no other verification that the hybrids produce viable seed. On June 19, 2003, some Lake Mead hybrids were producing flowers, but none of them appeared to have set seed. At the same time, there were no flowers (pollen sources) on nearby athel or saltcedars (J.G. personal observation). The lower water levels of Lake Mead have reduced flowering and seed set in athel (Barnes 2003). If the lake level is raised, or if athel establish at lower shoreline elevations (with better access to soil moisture), then increased flowering may provide more opportunities for hybridization or backcrossing. On August 15, 2003, hybrids at the Gila River site had mature flowers, but none appeared to have successfully set seed (R. Laugharn, personal observation).

Athel is presumably limited in latitudinal range by frost intolerance, and is rarely seen north of southern Utah (approximately 38°N lat.; Welsh et al. 1993) in the Colorado River watershed, or north of Las Cruces, NM (approximately 33°N lat.; Allred 2002) in the Rio Grande watershed. Saltcedar does not have such severe frost limitations and is found as far north as 52°N lat. in Asia (Baum 1978), and naturalized as far north as 48°N lat. in North Dakota (specimen *Mayer 20* (USDA-ARS-NPARK)), with cultivated plants extending into Canada (Kartesz and Meacham 1999; Pearce and Smith 2003). There are many locations where saltcedars and athel are sympatric in the USA, and the authors have searched for hybrids at several of these locations in California, Arizona, New Mexico, and Texas. However, the hybrid has only been confirmed from the three areas mentioned in this paper. Apparent morphological intermediates were

also observed within the Colorado River bottomland east of Needles, CA (elevation ca. 190 m) but were not collected nor included in this study.

The flowering phenologies of the parental species are different, but overlapping. The saltcedars flower from early spring to late fall, while athel flowers later in the year, from the end of summer to early winter (Baum 1978) (also see Barnes 2003 for athel phenology in the Lake Mead area), leaving ample opportunity for gene flow between saltcedars and athel. The late-season seed dispersal phenology of athel may contribute to the apparently infrequent seed reproduction of this species, and therefore of the hybrid we have described here, given the apparent maternal origin of the hybrid seed. Successful *Tamarix* seed germination generally requires bare, moist substrates, which are less likely to occur on river floodplains in the Sonoran or Mojave deserts in fall months than other times of the year, except perhaps following flooding associated with occasional tropical storms (Ely et al. 1994). Further, for seedling establishment to occur in North America, fall season germinants need to survive the winter months. Although low temperatures rarely drop below freezing at the sites we studied, we speculate that an inability to overwinter successfully may inhibit establishment of hybrid seedlings.

Even though it is unclear if the new hybrids can commonly reproduce by seed, one of the parental species is an athel that has chloroplast and nuclear marker genotypes identical to those invading Australia, and some of the other parental species are genetically identified as the most common invasive saltcedars in the USA (genotypes 1/1, 1/2, and 2/2 (Gaskin and Schaal 2002)). The tree habit of athel, combined with aggressive characteristics of the shrub saltcedar, could potentially produce an invader that is able to compete in ways different from saltcedar with native and naturalized riparian vegetation (e.g., increased height, increased phenological range, resistance to natural and imported enemies, etc.). On the other hand, genetic combinations associated with hybridization can often result in less competitive offspring, and failure of hybrid lineages in natural settings is undoubtedly underestimated due to our inability to detect such events. We suggest that the new *Tamarix* hybrids we report here should be investigated further for pollen and seed viability, and closely monitored for their ability to spread.

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COMPOSITION AND DYNAMICS OF THE SEED BANK OF COASTAL SCRUB IN BAJA CALIFORNIA

MARÍA DE JESÚS ANGOA-ROMÁN

Facultad de Ciencias, Universidad Autónoma de Baja California, Apartado Postal 1880, 22800 Ensenada, Baja California, México

STEPHEN H. BULLOCK¹

Departamento de Biología de la Conservación, Centro de Investigación Científica y de Educación Superior de Ensenada, Apartado Postal 2732, 22800 Ensenada, Baja California, México, and

Biology Department, San Diego State University, San Diego, CA 92182

TOANA KAWASHIMA

Statistical Consulting Center, San Diego State University,
San Diego, CA 92182

ABSTRACT

Seed bank dynamics are a critical consideration for management of arid and semi-arid shrublands. In the threatened “coastal succulent scrub” vegetation (at Punta Banda, Baja California), we studied the seed bank’s composition and size, as well as its dynamics as shown by field emergence and as inferred from literature reports on germination. We also analyzed sampling effort for both seeds and seedlings. The seed bank was sampled just prior to the rainy season, with 130 soil units of 7-cm diameter \times 1-cm depth distributed systematically over 1.66 ha. The field samples were mixed together then laboratory samples (17 of 14 cm³) were taken for manual extraction of seeds. We found 25 species, mostly of short-lived herbs. Some obvious species of the local flora were not encountered. Overall density was approximately 11,807 seeds m⁻², but densities differed by more than 100-fold among species. Analysis of sampling effort suggested that only 8–12 laboratory samples were needed to approach estimated asymptotes of the density of seeds and the number of species. Seedling emergence was recorded during four months on 30 randomly distributed and caged plots of 361 cm². We found 22 species, mostly short-lived herbs. Most species were uncommon and the density per plot of all species was highly skewed. Modes per plot were 3–4 species and 129–256 seedlings. Analysis of sampling effort suggested approximately 15 plots were needed to approach estimated asymptotes of the density of seedlings and the number of species. Published information on seed germination was found for 75 species which have been reported from coastal succulent scrub in the Punta Banda area. Apparently, fire-related cues were required for germination in only 13% of these, while most species may require only moist winters. However, long-term dynamics of the seed bank, and its geographic variation, remain to be studied.

RESUMEN

La dinámica del banco de semillas es un tema crucial para el manejo de matorrales de zonas áridas y semi-áridas. Estudiamos el tamaño y la composición del banco de semilla de matorral costero suculento en Punta Banda, Baja California. También observamos su dinámica, en la aparición de plántulas en el campo e inferida de reportes en la literatura sobre la germinación. Analizamos el efecto del esfuerzo de muestreo, ya que es el primer estudio del banco de semillas en matorral costero mediterráneo. El banco de semillas fue muestreado justo antes de la temporada de lluvias, con 130 unidades de 7 cm día \times 1 cm de profundidad y distribuidas sistemáticamente sobre 1.66 ha. Las muestras de campo fueron mezcladas, luego se tomaron muestras de laboratorio (17 de 14 cm³) para extraer las semillas manualmente. Encontramos 25 especies, principalmente de hierbas de corta vida; no se encontraron varias especies conspicuas de la vegetación local. La densidad general fue aproximadamente 11,807 semillas m⁻², pero entre las especies las densidades variaron por más de un factor de 100. Análisis del esfuerzo de muestreo sugirió que el número de especies y la densidad total de semillas fueron adecuadamente estimados con 8–12 muestras de laboratorio. La aparición de plántulas fue registrada durante cuatro meses en 30 cuadrantes enjaulados (de 361 cm²) distribuidos aleatoriamente. Encontramos 22 especies, principalmente de hierbas de corta vida. En su mayoría, las especies fueron escasas y la densidad total por cuadrante fue altamente sesgada; se presentaron modas de 3–4 especies y 129–256 plántulas. El análisis del esfuerzo de muestreo sugirió un muestreo adecuado con 15 o más cuadrantes. Se encontró información publicada sobre la germinación de 75 especies que se encuentran en el matorral costero suculento del área de Punta Banda. Disparadores de la germinación relacionados con incendios fueron reportados, como obligatorios,

¹ Author for correspondence, e-mail: sbullock@cicese.mx

en sólo el 13% de las especies. Aparentemente la mayoría de las especies germinan con cualquier invierno húmedo. No obstante, la dinámica a largo plazo de las especies y la biología de sus semillas, quedan por investigarse.

Key Words: coastal scrub, biodiversity, fire, germination, México, sampling, seed bank, vegetation dynamics.

Adequate management of mediterranean-climate shrublands requires an understanding of their diversity in the dimensions of physiognomy, floristics, environment, and dynamics. Among the features that distinguish California coastal scrub (Mooney 1977; Pase and Brown 1982; O'Leary 1990) from chaparral are the dominance of drought-deciduous shrubs (Harrison et al. 1971; Westman 1983), greater diversity of functional types across the geographic range of the vegetation (Peinado et al. 1994), and susceptibility to transformation from the combined effects of invasion and fire (Kirkpatrick and Hutchinson 1980; Minnich and Dezzani 1998). This vegetation is generally regarded as threatened or endangered in both Alta and Baja California due to increasing pressures of invasion and anthropogenic fire, together with urban development, agriculture and grazing (Westman 1981; O'Leary and Westman 1988; O'Leary 1990; Genin and Badán-Dangon 1991; Espejel 1993; Minnich and Dezzani 1998).

Nonetheless, information on the biology of the dynamics of California coastal scrub is scant, compared to the adjacent chaparral vegetation, and mostly refers to response to extreme stress (anthropogenic fire) in the Venturan and Riversidian associations in Alta California (reviewed in O'Leary 1990; see also DeSimone and Zedler 1999). In the chaparral, many species of shrubs and herbs are known to have large seed banks which can persist for many years, and to have germination improved by, or perhaps limited to, burned conditions (Sweeney 1956; Zammit and Zedler 1988, 1994; Parker and Kelly 1989; Keeley 1991). Of course, neither of these characteristics is universal among chaparral species, but they are sufficiently common that the dynamics of the vegetation is usually discussed in relation to a "fire cycle." For coastal scrub, we are unaware of direct data on community seed banks.

In coastal sage scrub, the continuous recruitment of shrubs and, apparently, of herbaceous perennials and some annuals suggest much of the system may be in flux in the absence of fire (Westman 1981; Malanson and O'Leary 1982; Keeley and Keeley 1984). Continuous regeneration is affected by disturbance of biotic origin and microlocal scale (DeSimone and Zedler 1999), and of course, "pyrophytes" are present at some sites. In the southern succulent variant of coastal scrub, the only study to date of regeneration was also initiated after a fire, but included all life forms and showed several modes of regeneration or life cycle strategies, including a few species that appeared to be fire de-

pendent (Cruz 1997). However, there has been no attention to the structure and dynamics of seed banks that must figure in regeneration of coastal scrub, in any of its various forms or environments. This paper aims to contribute to the understanding of the dynamics of coastal succulent scrub through investigation at one site in Baja California. We studied the size and composition of the seed bank and seedling emergence in undisturbed conditions, and also compiled published information on the germination of species found at or near our site, based on horticulture, experimental studies and field observations (although in most cases the seed provenance or site was more than 100 km distant from our field site).

Of course, the study of organisms in soil involves inherently difficult problems of sampling. Although it was not our purpose to compare different sampling techniques, an evaluation of different sampling intensities was an important goal, for both the seed bank and *in situ* germination. In this context, we made some methodological innovations that may facilitate other studies (and their comparison), and also found some provocative results that beg further basic study and contribute to discussions of management.

METHODS

The study site was on the small peninsula of Punta Banda in the State of Baja California, México, at about 31°43'48"N, 116°43'12"W and ca. 100 m elevation (Fig. 1). In the context of broad geographic variation in coastal scrub, our site was in the coastal succulent scrub formation and the Martirian association of Westman (1983). It was intermediate between the Diegan coastal sage scrub and Martirian coastal succulent scrub of Zippin and Vanderweir (1994), and corresponded roughly to the *Berberocactus emoryi*-*Agave shawii* association of Peinado et al. (1995) although *B. emoryi* was rare. The site does not correspond well to any of the California floristic series in Sawyer and Keeler-Wolf (1995). The most common perennials at our sample points were *Eriogonum fasciculatum*, *Agave shawii*, *Viguiera laciniata*, *Artemisia californica*, *Simmondsia chinensis*, and *Dudleya* spp.; less common species were *Euphorbia misera*, *Lotus scoparius*, *Rhus integrifolia*, *Mammillaria dioica*, and species of *Hazardia* and *Isocoma*; rare perennials included *B. emoryi*, *Salvia munzii*, *Ferocactus viridescens*, and *Cneoridium dumosum*. Grasses were noted at less than 11% of the points. Sampling of our site and others in the same association on Punta Banda was also done by Espejel (personal

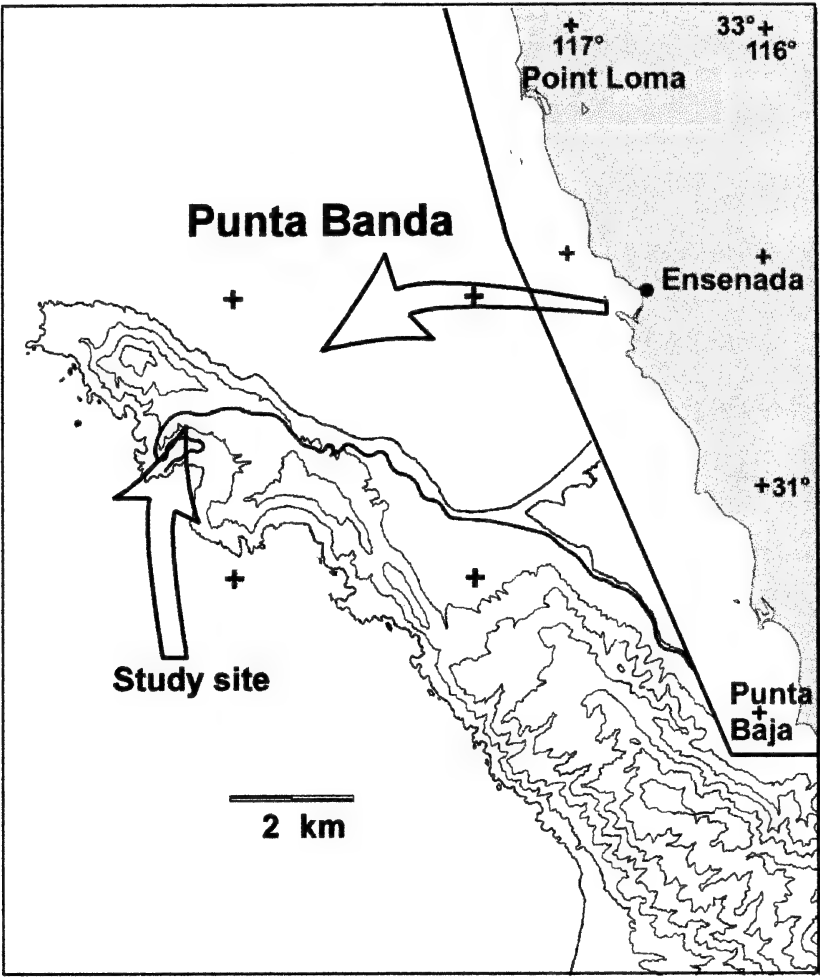


FIG. 1. Maps of Punta Banda, showing location of the study site, and of the region with Diegan and Martirian coastal scrub, showing the location of Punta Banda.

communication). A floristic list for Punta Banda (covering >3000 ha and including other vegetation types) was published by Mulroy et al. (1979). Nomenclature here follows Hickman (1993).

We chose our site from among accessible south-facing slopes, without appreciable ravines or ridges over at least one hectare, and within the largest patch of well-preserved vegetation. The topographic conditions probably supported a less-diverse flora than might be found on more rugged or moister areas of the point. There were no signs of trails, roads or former structures, and only scant and aged signs of livestock and some exotic flora. There were no signs of recent fire, and mapping from aerial photographs suggested no fires in at least 40 yr (R. Minnich personal communication). Rocks of porfite and andesite littered much of the site. Soil analysis showed moderately acid conditions ($\text{pH } 5.57 \pm 0.4$ [SD]; $n = 9$) with variable organic carbon (1.85–6.23%), a clay fraction of $29.19 \pm 1.92\%$ and a sand fraction of $32.97 \pm 2.75\%$. Climatic data

were available for Ensenada, ca. 17 km NNE of the site. There, annual precipitation averaged 271 mm (range 102–612, for 68 yr between 1894 and 1998), and monthly mean temperatures ranged from 7 to 14°C.

Field soil samples were taken at the end of October 1993, before the first winter rains, on a plot of 104 m by 160 m at alternate points on an 8 m grid, so there were 130 samples. Each sample was 7 cm in diameter and 1 cm deep (or less in the presence of rocks). After removal of rocks, sticks, leaves, roots, *Selaginella* and feces, the field samples were thoroughly mixed together using a gem-grinding drum. The bulk lot amounted to 3.370 liters and 4.744 kg. Laboratory samples of 14 cm³ were taken from this bulk lot, and propagules were separated with dissecting needles under a microscope. Species were identified from reference collections and with the assistance of a specialist. Emergence of seedlings was observed in the field between January and May (1994), in 30 plots of

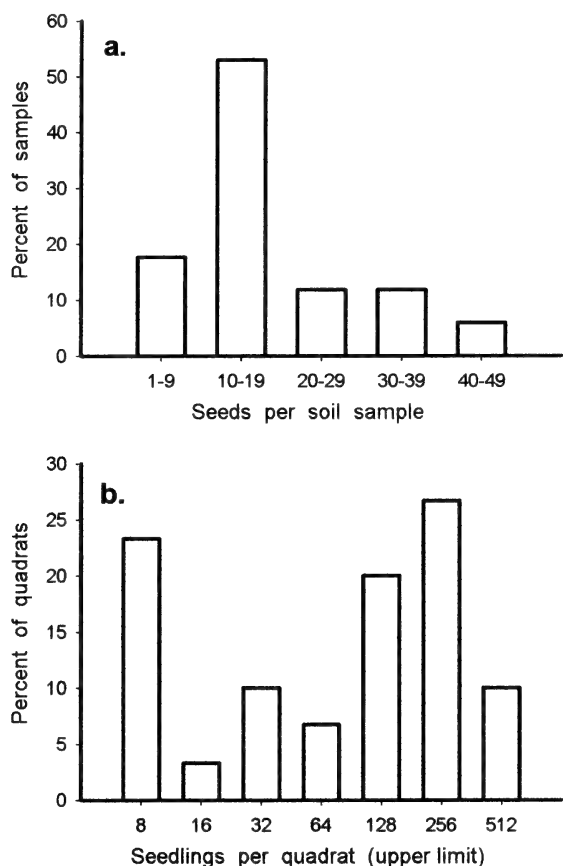


FIG. 2. Frequency distributions of a) number of seeds per aliquot of the mixed soil sample, and b) number of seedlings per quadrat.

19 cm by 19 cm, distributed at random over the same area from which the soil was sampled, with each plot protected by a hard wire cage, 5 cm high with 1 cm mesh. Unfortunately, due to technical problems it was not possible to identify all seed or seedling species.

The effect of cumulative number of samples on cumulative number of species and total species richness, were examined for both the seed bank and seedling data using the EstimateS software of Colwell (2000). Indices reported and discussed here are the S_{obs} , Jack 1 and Chao 2. The ICE index is not presented here for three reasons: its definition changes at 10 samples; its error goes to zero as cumulative number of samples approaches the maximum; and its behavior with our data was not close to a monotonic increase. For each index and data set, 50 randomizations of sample order were examined, without replacement.

RESULTS

Seeds in Soil

A total of 17 laboratory samples of soil were examined, yielding 281 seeds of 25 species. The

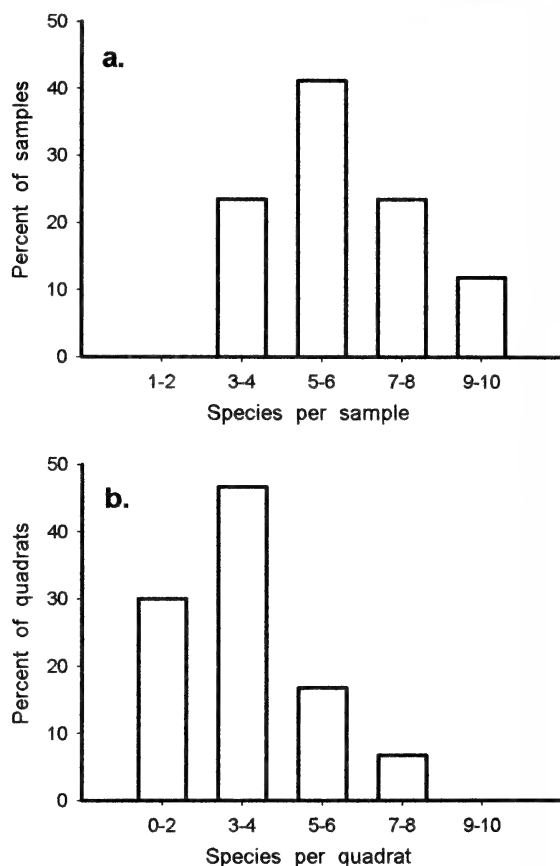


FIG. 3. Frequency distributions of a) number of species of seeds per aliquot of the mixed soil sample, and b) number of species of seedlings per quadrat.

number of seeds per sample was not normally distributed despite prior mixing, but there were no samples without seeds (Fig. 2a). The modal category was 10–19 seeds. The number of species per sample ranged from three to nine with a mode of 5–6 (Fig. 3a). Nine morphospecies could not be identified to family and five others were identified only to family level. We encountered seeds of two cactus species, as well as four Asteraceae and three Poaceae, probably all natives. The only dominant shrub encountered was *Eriogonum fasciculatum*.

Almost two-thirds of the species were represented by a total of less than four seeds in the 17 samples (Fig. 4a). The most abundant seeds were of *Crassula connata* (49% of the total), *Hemizonia* sp. (14%) and *E. fasciculatum* (9%). Notably, sporocarps of *Selaginella* species were almost as abundant as *C. connata* seeds. Seed size among the species encountered ranged from 0.25 to 2.8 mm in the longest dimension.

Seedlings

In the 30 protected plots, we recorded a total of 3148 seedlings of 22 species. The range was zero

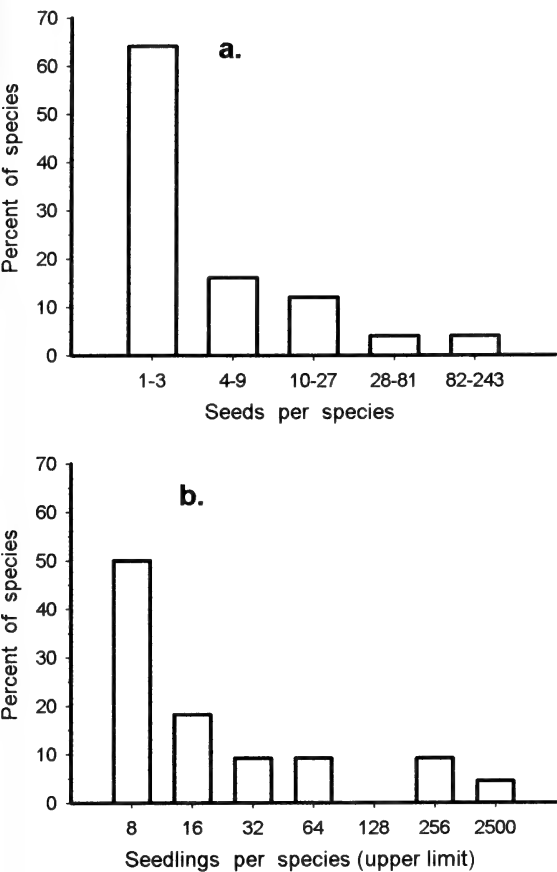


FIG. 4. Frequency distributions of a) total number of seeds per species in all aliquots of the mixed soil sample, and b) total number of seedlings per species in all quadrats.

to 512 seedlings per plot and the distribution was extremely skewed (Fig. 2b). More than a third of the plots contained fewer than 64 seedlings, but about a third of all the seedlings occurred in just 10% of the plots. The number of species per plot ranged from zero to seven, with a mode of 3–4 (Fig. 3b). Three morphospecies, represented by a total of 11 seedlings, were not identified to family, and seven were identified only to genus. The family with the most species was Asteraceae (six), followed by Poaceae and Polemoniaceae (three each), Crassulaceae and Scrophulariaceae (two), and Brassicaceae, Fabaceae and Valerianaceae (one). Only two of the identified species were perennials (*Festuca* sp. and *Dudleya lanceolata*), and only one was clearly not native (*Sonchus oleraceus*).

More than 68% of the species were represented by a total of less than 17 seedlings in the 30 plots (Fig. 4b). On the other hand, the most abundant species was *C. connata* that accounted for 78% of all seedlings and occurred in 63% of the plots. The next most abundant species were *Navarretia atractyloides* and *Festuca* sp., accounting for an addi-

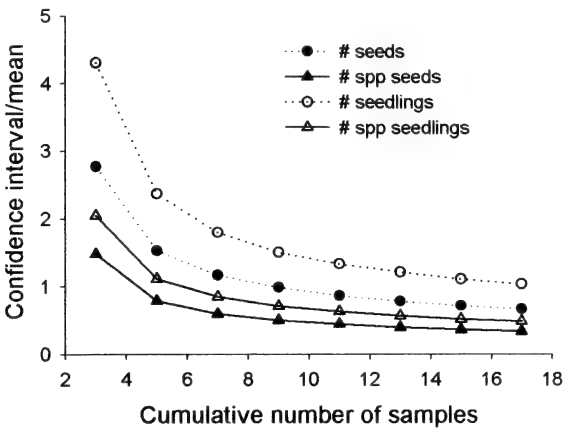


FIG. 5. Effect of cumulative sample size on the ratio of confidence interval to mean (bootstrapped trends).

tional 14% of all seedlings. The exotic *S. oleraceus* accounted for 0.3% of all seedlings and occurred in 17% of the plots.

Sample Size

To examine the effect of the number of samples on estimates of the mean number of individuals and of species per sample unit for both the seed bank and seedlings, confidence intervals were estimated for a range (≥ 3) of cumulative number of samples, using bootstrap techniques. The ratio of confidence intervals to means showed a smooth progression in all cases (Fig. 5): ratios were larger for number of individuals than for number of species, although means were much larger for individuals, and ratios were larger for seedlings than for seeds. The decline of the ratios appeared to be asymptotic.

The effect of cumulative number of samples on estimates of accumulated and total number of species of seeds and seedlings was examined with three indices (Fig. 6). S_{obs} showed the slowest rise in cumulative number of species; this index was not asymptotic but necessarily reached the total numbers of species observed at the full sample sizes for seeds and seedlings. Jack 1 started at similar values to S_{obs} but rose more quickly and to higher values. It reached an asymptote of about 30 species at about 12 samples for the seed bank; for seedlings, Jack 1 showed most species were found within 19 quadrats, but the curve continued to increase slowly even above 27 species in 25 quadrats. Compared to Jack 1, the Chao 2 index estimated more species at a smaller cumulative number of samples but the asymptotes were lower; it also reached asymptotes sooner, at about 8 samples for seeds and about 14 for seedlings. Chao 2 estimated that there should be a total of about 26 species in both cases, which was an interesting coincidence given the independent sampling of seeds and seedlings.

TABLE 1. EVIDENCE FOR HEAT EFFECT ON GERMINATION OF COASTAL SUCCULENT SCRUB SPECIES. The floristic list for Punta Banda derives from Mulroy et al. (1979) and Espejel (personal communication). Germination information is for seeds from other provenances in horticultural treatment or experiments, reported by 1) Emery (1988) and 2) Keeley (1991), or from field observations by 3) DeSimone and Zedler (1999) and 4) this study. Symbols: -, germination without a fire-related stimulus; +, germination with fire-related stimulus or alternative seed-coat softening factors; ±, mixed or conflicting results.

| Family | Species | Heat effect | Sources |
|------------------|-----------------------------------|-------------|---------|
| Liliaceae | <i>Agave shawii</i> | - | 1 |
| | <i>Allium praecox</i> | - | 2 |
| | <i>Calochortus splendens</i> | - | 1, 2 |
| | <i>Dichelostemma capitatum</i> | - | 1, 2 |
| | <i>Zygadenus fremontii</i> | - | 1, 2 |
| Poaceae | <i>Achnatherum coronatum</i> | - | 1, 2 |
| | <i>Muhlenbergia microsperma</i> | - | 4 |
| | <i>Nassella cernua</i> | - | 1 |
| | <i>Nassella pulchra</i> | - | 1, 2 |
| | <i>Poa secunda</i> | - | 1 |
| Anacardiaceae | <i>Vulpia octoflora</i> | - | 4 |
| | <i>Malosma laurina</i> | + | 1, 2 |
| | <i>Rhus integrifolia</i> | + | 1, 2 |
| Asteraceae | <i>Artemisia californica</i> | ± | 2, 3 |
| | <i>Coreopsis maritima</i> | - | 1 |
| | <i>Encelia californica</i> | - | 1, 2 |
| | <i>Gnaphalium bicolor</i> | - | 1 |
| | <i>Gnaphalium californicum</i> | ± | 2, 4 |
| | <i>Hazardia orcuttii</i> | - | 1 |
| | <i>Ericameria palmeri</i> | - | 1 |
| | <i>Isocoma menziesii</i> | - | 1, 2 |
| | <i>Heterotheca grandiflora</i> | - | 2 |
| | <i>Filago arizonica</i> | - | 4 |
| | <i>Lasthenia californica</i> | - | 4 |
| | <i>Porophyllum gracile</i> | - | 1 |
| | <i>Rafinesquia californica</i> | + | 2 |
| | <i>Trixis californica</i> | - | 1 |
| Boraginaceae | <i>Cryptantha intermedia</i> | + | 2 |
| Brassicaceae | <i>Descurainia pinnata</i> | - | 2 |
| | <i>Lepidium nitidum</i> | ± | 2, 4 |
| | <i>Streptanthus heterophyllus</i> | + | 2 |
| Cactaceae | <i>Ferocactus viridescens</i> | - | 1 |
| Capparidaceae | <i>Cleome isomeris</i> | - | 1 |
| Caryophyllaceae | <i>Cardionema ramosissimum</i> | - | 1 |
| | <i>Spergularia macrotheca</i> | - | 1 |
| | <i>Atriplex canescens</i> | - | 1 |
| Chenopodiaceae | <i>Calystegia macrostegia</i> | ± | 1, 2 |
| Convolvulaceae | <i>Crassula connata</i> | - | 4 |
| Crassulaceae | <i>Dudleya lanceolata</i> | - | 1, 4 |
| | <i>Marah macrocarpus</i> | - | 1, 2 |
| Cucurbitaceae | <i>Acalypha californica</i> | - | 1 |
| Euphorbiaceae | <i>Chamaesyce polycarpa</i> | - | 1 |
| | <i>Aesculus parryi</i> | - | 1 |
| Hippocastanaceae | <i>Emmenanthe penduliflora</i> | + | 1, 2 |
| Hydrophyllaceae | <i>Phacelia cicutaria</i> | ± | 1, 2 |
| | <i>Phacelia parryi</i> | + | 2 |
| | <i>Lotus strigosus</i> | + | 1, 2 |
| Fabaceae | <i>Lotus hamatus</i> | + | 1 |
| | <i>Lotus salsuginosus</i> | + | 2 |
| | <i>Lotus scoparius</i> | ± | 1, 4 |
| | <i>Lupinus bicolor</i> | + | 1 |
| | <i>Lupinus hirsutissimus</i> | + | 1 |
| | <i>Lupinus longifolius</i> | + | 1 |
| | <i>Lupinus sparsiflorus</i> | + | 1 |
| | <i>Lupinus truncatus</i> | + | 1 |
| | <i>Salvia apiana</i> | ± | 1, 2, 3 |
| | <i>Malacothamnus fasciculatus</i> | + | 2 |
| Lamiaceae | <i>Mirabilis californica</i> | - | 1 |
| Malvaceae | <i>Clarkia epilobioides</i> | + | 2 |
| Nyctaginaceae | | | |
| Onagraceae | | | |

TABLE 1. CONTINUED.

| Family | Species | Heat effect | Sources |
|------------------|--------------------------------------|-------------|---------|
| Polemoniaceae | <i>Linanthus</i> sp. | – | 4 |
| | <i>Navarretia atractyloides</i> | – | 4 |
| | <i>Navarretia</i> sp. | – | 4 |
| Polygonaceae | <i>Eriogonum fasciculatum</i> | – | 1, 2, 3 |
| | <i>Eriogonum grande</i> | – | 1 |
| Portulacaceae | <i>Claytonia perfoliata</i> | – | 1 |
| Primulaceae | <i>Dodecatheon clevelandii</i> | – | 1 |
| Rubiaceae | <i>Galium angustifolium</i> | + | 2 |
| Rutaceae | <i>Cneoridium dumosum</i> | – | 1, 2 |
| Scrophulariaceae | <i>Antirrhinum kelloggii</i> | – | 4 |
| | <i>Castilleja exserta</i> | – | 1 |
| | <i>Castilleja foliolosa</i> | – | 1 |
| | <i>Linearia canadensis</i> | – | 4 |
| | <i>Mimulus aurantiacus</i> | – | 1, 2 |
| Simmondsiaceae | <i>Simmondsia chinensis</i> | – | 1 |
| Valerianaceae | <i>Plectritis</i> cf. <i>ciliosa</i> | – | 4 |

Germination

Reports concerning conditions for seed germination have been found for 75 species of the flora of Punta Banda coastal scrub. Table 1 summarizes this information with regard to whether seeds may commonly germinate with only climatically-typical conditions of moisture and temperature. The particular concern is whether heat or some fire-related factor is necessary for germination. The information is based in part on experimental studies of germination in species that occur in chaparral (Keeley 1991), and in part on horticultural experience and experiments (Emery 1988). Additional information came from our and others' recent field observations (Cruz 1997; DeSimone and Zedler 1999).

According to our review, about 75% of the species in our extended-local flora will germinate without a fire-related stimulus (– in Table 1). The literature suggests that some species have multiple mechanisms for germination, e.g., softening of the seed coat is an alternative to fire-related factors (+ in Table 1); however, the natural history interpretation remains obscure. There are also some taxa that have given either mixed or conflicting results (± in Table 1; see also Keeley 1986).

DISCUSSION

Overall, the seed bank was not impressively large for the available space or in comparison with chaparral (Zammit and Zedler 1988) or with North American warm deserts (Kemp 1989). Our data suggest an overall density of only 1.2 seeds cm⁻², or about 11,807 seeds m⁻², and about 26–30 species. Also, the abundance of seeds varied among species by more than two orders of magnitude, so that most species were quite rare. The great variation among sympatric species and among habitats in mediterranean climate areas has been emphasized by other authors (Parker and Kelly 1989, Zammit and Zedler 1994). Apparently, the present

study is the first in any type of coastal scrub in the California bioregion; as such, the field results should not be considered representative of coastal scrub.

The seed bank, seedling and annual vegetation, and mature perennial vegetation differed strikingly in composition, with perhaps two exceptions. Both the seed bank and seedling vegetation were largely dominated by *Crassula connata*, a diminutive annual succulent with very small seeds, and other annual herbaceous species. We did not encounter seeds of most species that were prominent in the vegetation (e.g., *Euphorbia misera*, which has explosive fruits, and *Artemisia californica*). One hypothesis might be that their seeds are short-lived and are not produced in abundance every year. The absence of seeds of some common perennials such as *Simmondsia chinensis*, *Agave shawii* and *Rhus integrifolia*, might reflect infrequent seed production, or might represent a relatively low reproductive output that is concentrated in larger and fewer propagules, which are correspondingly rarer. Larger seeds may also be more susceptible to predation. In contrast, *Eriogonum fasciculatum*, a common shrub with seeds roughly 1.5–2 orders of magnitude smaller in volume than the above species, was apparent in the seed bank but absent among the seedlings. Altogether, this relatively uniform and stressful site showed a small flora below ground as well as above.

Sampling of seed banks is generally neglected because of its inherent difficulties. Our procedure may allow a site-level rapid assessment: we collected only 0.003% of the site surface, and examined only 4.8% of that collection, but we estimated that species number was asymptotic species numbers after about 59% of that sample. Undoubtedly species were missed with this procedure, as with any other, and sampling at one or two orders of magnitude greater intensity would reveal species that are rare in the seed bank (whether common or

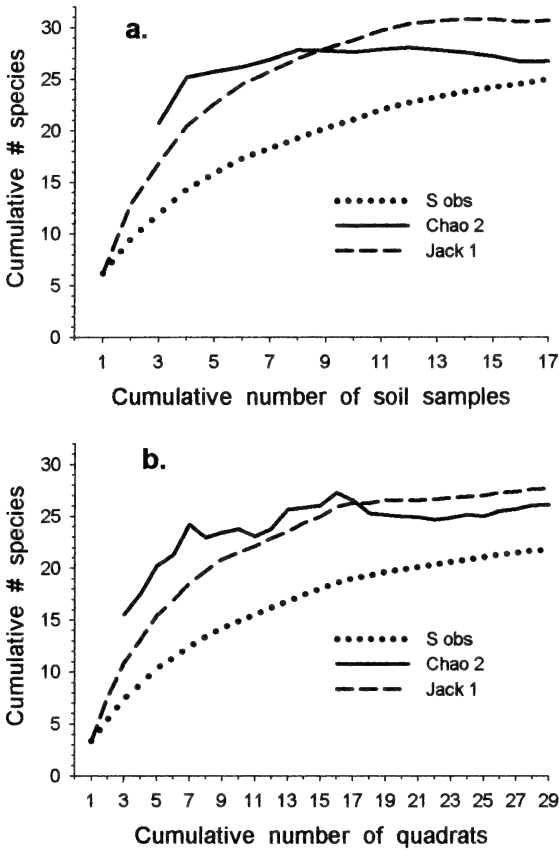


FIG. 6. Effect of cumulative sample size on indices of cumulative number of species of a) seeds and b) seedlings.

rare in the vegetation). Nonetheless, we suggest that eliminating spatial variability from the seed bank provides a useful simplification for survey and comparative studies of species number, composition and seed density, particularly for herbaceous species. The seedling data suggest that seed distribution is heterogeneous and not "normal," so bulk-ing the field samples should improve the chances of finding less common species, and provide a site-level estimate of density. Of course, sites with greater variation in cover, drainage, slope and exposure may require a greater intensity or different structure of sampling and analysis.

The depth of our sampling may be a concern, particularly if the seed rain differs much across years, or if seed predators are selective of species that may slowly build a large seed bank due to multi-year dormancy. Moreover it would be useful to investigate whether species in the near-surface seed bank, which is susceptible to erosion and to destruction in fires, are also at greater depth. However, a sampling protocol with a greater fixed depth would have required much rock chiseling and/or crevasse cleaning in our case, and a protocol of variable depth creates problems with extrapolation to surface area.

The estimate of the total number of species in a community depends to some extent on the choice of statistical procedure. The simple and infrequently-used bootstrap procedure (S_{obs}) suggested sampling was not adequate for either seeds or seedlings. In contrast, the more widely-used procedures of Jack 1 and Chao 2 suggested our sample size was more than adequate for seeds and adequate for the seedling community. However, these two procedures differed substantially in estimates for the asymptotic number of species of seedlings, a result which was probably due to the non-uniform distributions of species and seedlings.

Although recent invasions and changes in land-use and culture will probably make fire an increasingly prominent factor (Keeley 1982; Minnich 1983; Minnich and Dezzani 1998; Keeley and Fotheringham 2001), the great majority (ca. 75%) of the species of coastal succulent scrub at Punta Banda probably germinate without a fire-related stimulus. Moreover, the list is certainly an underestimate and could reasonably be augmented with other species based on the consistency of these characters with respect to taxonomy and life form (e.g., most Asteraceae, Cactaceae, Poaceae, *Dudleya*, *Allium*, *Jepsonia*). What fraction of the seed bank is actually dormant remains to be determined. Field germination might have amounted to ca. 25% of the seed bank in our case, based on an estimate of 2907 seedlings m^{-2} (although this is based on a very non-normal distribution). A particularly curious case was the absence of *E. fasciculatum* from the seedlings, despite its present in the seed bank.

The reports on germination requirements of some species show mixed or conflicting results, which suggest that either germination occurs to some extent without fire but is augmented by fire (e.g., Stone and Juhren 1951, 1953), or that seed age and condition may be complicating factors (Odion 2000), or that geographic variation may be significant. Most of the information in Table 1 derives from seeds from localities other than our study site, although this is standard usage. Remarkably, geographic (and particularly historical) variation in germination characteristics has been ignored in shrubland species of the Californian bioregion, with rare exception (e.g., Capon and Brecht 1970; Keeley 1986). Variations within plants or with populations have fared only slightly better (Cook et al. 1971; Zammit and Zedler 1988, 1994). Unfortunately, despite the interest of Baja California as a biological and climatic transition zone (Shreve 1936; Bullock 1999), we know of no studies on germination from Baja California populations in coastal scrub or chaparral. Some species which are supposed to have large and persistent seed banks elsewhere, were not apparent in the seed bank at our site despite presence (if not abundance) of the plants. This may be another indication that seed biology is not necessarily homogeneous, although

it would be premature to speculate about specific factors.

Apparently, the seed bank is a limited asset for conservation management in the face of pastoral-agriculture uses and suburban-urban development. For the restoration of disturbed or denuded sites, movement of soils would not be efficient for establishing vegetation structure but might have some interest for introduction of the herbaceous flora. Also, the superficial seed bank we studied might be largely lost in severe fires or with the typical pre-construction razing of the surface. Fire, overwhelmingly anthropogenic, is a dramatic and powerful force in reorganizing coastal scrub in general (O’Leary 1990; Cruz 1997). The weight of evidence suggests an appreciable element of the coastal succulent scrub in our area is dependent on fires for germination, but the vast majority of species are not. In an average winter, germination was abundant but showed mostly annual species, in terms of numbers of individuals and of species. Moreover, most of the dominant shrubs did not form large, dormant seed banks, unlike the common conception of some major species of the chaparral (Parker and Kelly 1989). The broader-scale, longer-term and contingent behavior of the seed bank remains to be studied, but we hope this initial exploration may serve to provoke and even instruct further study.

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THE INFLUENCE OF SEED DISPERSAL AND PREDATION ON FOREST ENCROACHMENT INTO A CALIFORNIA GRASSLAND

PETER G. KENNEDY¹ AND JESSICA M. DIAZ

Department of Integrative Biology, University of California, Berkeley, CA 94720

ABSTRACT

Forest encroachment into grasslands is a widespread phenomenon with significant implications for land management. We examined the influence of seed dispersal and predation on the encroachment of two tree species, *Lithocarpus densiflora* and *Pseudotsuga menziesii*, into a coastal California grassland. We mapped the distributions of *L. densiflora* and *P. menziesii* seedlings and saplings and *L. densiflora* acorns across the forest-grassland ecotone as well as quantified the fates of seeds of both species experimentally located at five distances across the ecotone. Species distributions varied, with *P. menziesii* being most abundant in the grassland and at the edge and *L. densiflora* in the forest. *Lithocarpus densiflora* acorns were absent from the grassland but equally abundant at the edge and forest. Seed predation was similar for both species, being low in the grassland, variable at the edge, and high in the forest. It appears that *L. densiflora* encroachment into the grassland is strongly influenced by seed dispersal, while *P. menziesii* encroachment is more likely influenced by seed predation than dispersal.

Key Words: forest-grassland ecotone, seed dispersal, seed predation, woody plant establishment, *Pseudotsuga menziesii*, *Lithocarpus densiflora*.

Woody plant-grassland ecotones have been postulated to remain stable for long ecological time periods (Griffin 1977; Davis and Mooney 1985); however, many studies have documented an increase in woody plant encroachment into grasslands in recent years (Van Vetgen 1983; Hobbs and Mooney 1986; Archer 1989; Trollope et al. 1989; Roques et al. 2001). A number of mechanisms have been proposed to explain the increase in encroachment including climate change (Poley et al. 1997), fire suppression (Bragg and Hurlbert 1976; Callaway and Davis 1993), succession (Archer 1988), and over-grazing (Archer 1995; Roques et al. 2001). While each of these factors can be important and they are not mutually exclusive, the specific determinants of woody plant encroachment often vary among environments (Scholes and Archer 1997).

In coastal California, fire was a primary historical factor controlling the stability of woody plant-grassland ecotones (Griffin 1977; Greenlee and Langenheim 1990; Keeley 2002). The high frequency of Native American burns and fires caused by lightning maintained a mosaic of grasslands, shrublands, and forests throughout the coastal region (Keeley 2002). Over the past two centuries, however, policies of fire suppression have effectively reduced fire frequency (Minnich 1983; Greenlee and Langenheim 1990), and this suppression has corresponded with the increase of woody plant encroachment into grasslands (McBride and Hady 1968; McBride 1974; Callaway and Davis 1993; Keeley 2002).

Although the absence of fire appears to be a key factor allowing for woody plant establishment in grasslands, a suite of other ecological factors can also influence encroachment dynamics (Scholes and Archer 1997). Much of the research in California has focused on the changes in light and soil moisture among grasslands and woody plant communities (Davis and Mooney 1985; Hobbs and Mooney 1986; Williams and Hobbs 1989; Muick 1991), the competitive interactions among woody plants and grasses (Griffin 1971; Gordon et al. 1989; Danielson and Halvorson 1991), and the effects of animal herbivory (Griffin 1980; Davis et al. 1991). In addition to these factors, other research outside California suggests that both seed dispersal and predation may also be important in controlling woody plant encroachment (Stapanian and Smith 1986; Brown and Archer 1987; Kollman and Schill 1996; Hubbard and McPherson 1999). While the relative significance of these different ecological factors is likely to vary among locations, factors affecting encroachment have also been shown to have hierarchical and interactive effects (House et al. 2003). Because seed dynamics can have a major influence of seedling distributions and abundances, analyzing this life stage in conjunction with later stages may be particularly important in understanding patterns of woody plant encroachment.

At our research site on Mount Tamalpais, California, where both fire and grazing have been excluded from the grasslands for the past 50 years (M. Swezy personal communication), there has been widespread woody plant encroachment (Fig. 1). The objective of this paper was to examine the influence of seed dispersal and predation on the en-

¹ Author for correspondence, e-mail: pkennedy@socrates.berkeley.edu



FIG. 1. Forest encroachment in the grasslands along Bolinas ridge, Mt. Tamalpais, CA (37°54'N, 122°37'W).

croachment of the dominant forest tree species, *Lithocarpus densiflora* (Hook. & Arn.) Rehder and *Pseudotsuga menziesii* (Mirbel) Franco, into the grassland. To quantify the rates of encroachment, we mapped the locations of *L. densiflora* and *P. menziesii* seedlings and saplings at five distances across the forest-grassland ecotone. We also quantified the natural acorn rain of *L. densiflora* at those distances and the movement of acorns placed at the forest edge. Finally, we experimentally manipulated the locations of *P. menziesii* seeds and *L. densiflora* acorns across the forest-grassland ecotone and followed their fate over five week periods.

METHODS

Study Area and Species

The study was conducted along Bolinas ridge in the Marin Municipal Water District watershed on Mount Tamalpais (37°54'N, 122°37'W) in southern Marin County, CA. The 9000-ha watershed encompasses a mix of vegetation types, including grassland, chaparral, and mixed evergreen forest (Parker 1991). The mixed evergreen forest is dominated by *P. menziesii* (hereafter referred to as *Pseudotsuga*) and *L. densiflora* (hereafter referred to as *Lithocarpus*), with *Quercus agrifolia* Nee, *Quercus chrysolepis* Liebm., *Arbutus menziesii* Pursh, *Umbellularia californica* (Hook. & Arn.) Nutt., and *Sequoia sempervirens* (D. Don) Endl. also present (Horton et al. 1999). The grasslands are a mixture of exotic annuals and native and exotic perennials dominated by *Danthonia californica* Boland, *Bromus carinatus* (Nutt. ex Buckl.) Shear, *Lolium multiflorum* Lam., and *Briza major* K.Presl (J. Corbin personal communication). The study area is characterized by a mediterranean climate with a seasonal summer

dry period and average annual precipitation of 1250 mm (Dunne and Parker 1999). Soils in the grassland are classified as composites of the Saurin clay loam and Bonnydoon gravelly loam series and in the forest, Centissima loam-Barnabe very gravelly loam series (U.S.D.A. 1990).

The two tree species disperse their seeds between August and December. *Lithocarpus* acorns can fall as early as late August, but early acorns are generally immature and insect infested (P. Kennedy personal observation). Mature acorns typically fall between late September and late November (Tappeiner et al. 1990). *Pseudotsuga* seeds fall rapidly after the cones mature and approximately two-thirds of the total seed crop is on the ground by late October (Hermann and Lavender 1990).

Seed size and dispersal method vary between species. *Lithocarpus* acorns range from 2–5 cm long \times 1–2 cm wide and are primarily small-mammal and bird dispersed (Tappeiner et al. 1990). The western grey squirrel (*Sciurus griseus*) is the primary disperser in the study area, although the Steller's jay (*Cyanocitta stelleri*) may also move acorns (P. Kennedy personal observation). Primary acorn predators include the aforementioned dispersers, the acorn woodpecker (*Melanerpes formicivorus*), and potentially the California mouse (*Peromyscus californicus*; see Kalcounis-Ruppell and Millar 2002 about *P. californicus*). Insects such as filbert weevils (*Curculio occidentalis*) are also important acorn predators (Lewis 1991); however, their effects were not addressed in this study. *Pseudotsuga* seeds are 6–12 mm long \times 2–4 mm wide and primarily wind-dispersed (Hermann and Lavender 1990). The seeds are consumed by a wide range of insect, small mammal, and bird species (Gashwiler

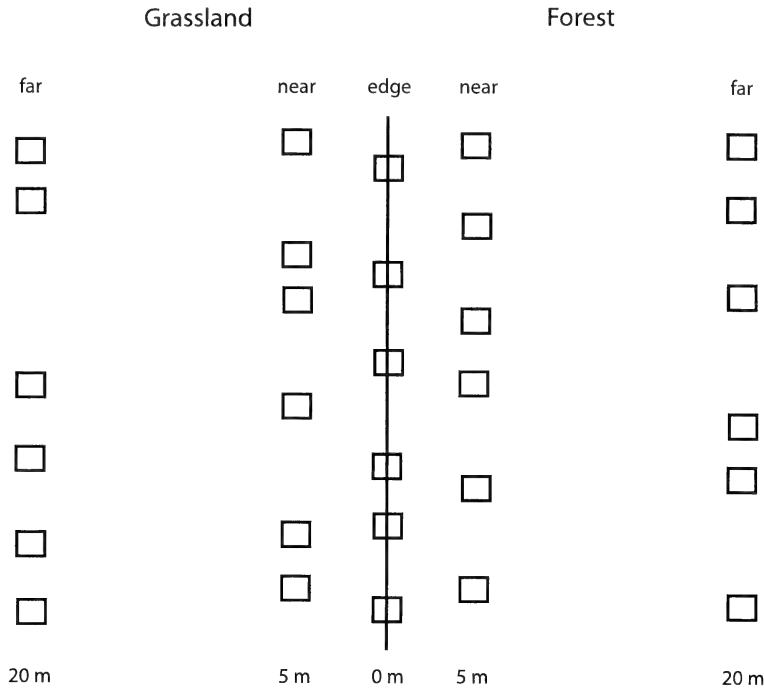


FIG. 2. Sampling design across the forest-grassland ecotone. The squares represent one m² plots randomly located at each distance. See text for details of plot replication.

1968). Due to differences in dispersal mode, we hypothesized that *P. menziesii* would have higher seed and therefore seedling and sapling densities in the grasslands than *L. densiflora*. Additionally, we hypothesized that the intensity of seed predation would be lower in the grasslands for both species because there is less vegetative cover to protect seed dispersers from predators.

Sampling and Experimental Design

Seedling and sapling distributions. In February 2003, we haphazardly selected five sites with evidence of woody plant encroachment. The sites were located 0.2–1 km apart. At each site, five distances across the forest-grassland ecotone were located: far grassland (20 m into the grassland), near grassland (5 m into the grassland), edge (at the forest-grassland ecotone edge), near forest (5 m into the forest), and far forest (20 m into the forest). The forest-grassland edge was defined as the location where the branches of forest trees were present at 2 m above the ground. In all cases, the edge was very easy to delineate given the large differences in age between trees in the forest and those in the grassland. At each distance, six 1-m² plots were randomly established along a 20-m transect running parallel to the ecotone edge (Fig. 2). Within each plot, all *Lithocarpus* and *Pseudotsuga* individuals less than ten cm diameter at breast height (DBH) were counted. Individuals were divided into two age classes: those with a DBH between one and ten

cm were considered saplings and those with a DBH less than one cm or without a DBH were considered seedlings. We first calculated the proportion of plots in which each species was present at each distance and site. Using site as the level of replication, we then conducted a two-way (species and distance) fixed factor analysis of variance (ANOVA) to analyze distributions across the ecotone (n = 25 plots per species). The variances were first determined to be homogenous using Cochran's C test (P > 0.05).

Acorn distributions. To sample *Lithocarpus* acorn distributions across the ecotone, we randomly selected different five sites that had at least one acorn-producing *Lithocarpus* individual in the forest canopy within 20 m of the ecotone edge. The sites were located 0.3–1.5 km apart. Using the identical sampling design as above, we counted the number of whole fallen 2002 acorns within each 1-m² plot on 1 November 2002 (distinguished from older acorns by color and surface texture). We used a two-way mixed model ANOVA, with site (random) and distance (fixed) as the model factors to analyze the acorn distributions (n = 150 plots). The data were first log(X + 1) transformed to make variances homogenous (Cochran's C test). Tukey HSD tests were used for *a posteriori* comparisons between means within each site.

Seed dispersal and handling experiment. In early October 2002, *Lithocarpus* acorns were collected along Bolinas ridge. In the laboratory, acorns were

immersed in water and all those floating after five minutes were considerable inviable (Nyandia and McPherson 1992). Viable acorns were surface sterilized in a 10% bleach solution for five minutes, air dried, and stored at 4°C for a week before tagging. All *Pseudotsuga* seeds were collected from a nearby coastal forest and provided by the U.S. Forest Service, Placerville nursery.

The acorn tagging method was modified from Forget et al. (1998). A 1-mm diameter hole was drilled through the center of the acorns and threaded with a 1-m piece of clear fishing line. The line was knotted on both sides of the acorn, and a small numbered tag was attached to the opposite end. *Pseudotsuga* seeds were not tagged due to their small size. Instead, they were individually placed on outer edge of 5 × 2.5 cm sticky whitefly cards (Safer Inc., Bloomington, MN) when put in the plots. The sticky cards were necessary because the *Pseudotsuga* seeds could not be relocated in the grasslands or forest floor without them. Although the sticky cards may have potentially altered the behavior of seed predators, all seeds were placed on sticky cards; therefore, their effect should be similar at all distances.

In mid-October 2002, two sites, separated by 1 km, were randomly selected. At both sites, the same far grassland, near grassland, edge, near forest, and far forest distances as above were located (Fig. 2). At each distance, a 50-m transect running parallel to the forest-grassland ecotone was delineated. Along each transect, 15 one-m² plots separated by least one m were established. The plots were randomly assigned as follows: six plots with tagged *Lithocarpus* acorns, three plots with untagged *Lithocarpus* acorns, and six plots for *Pseudotsuga* seeds ($n = 90$ *Lithocarpus* plots and $n = 60$ *Pseudotsuga* plots). Within the acorn plots, eight acorns were randomly located on the soil surface ($n = 720$ acorns total). In the *Pseudotsuga* plots, four seeds (each on an individual sticky card) were put on the soil surface at the four corners of the plot ($n = 240$ seeds total).

Lithocarpus acorns were put out from October 15–November 15 and *Pseudotsuga* seeds November 10–December 10. Each acorn and seed was scored as “handled” or not. Handling was defined as eaten, buried, moved, or disappeared. Although some of the buried, moved, or missing acorns may have escaped predation, the number of moved and missing acorns was low, and many studies have shown that the majority of buried acorns are eventually eaten (see Van der Wall 2001). Therefore, we consider handling to be a maximum estimate of predation. We could not determine the fate of untagged but handled acorns or *Pseudotsuga* seeds and therefore scored these only as handled or not. Seed handling was calculated as the proportion of seeds handled in each plot.

Pooling the tagged and untagged acorn data (a prior analysis showed no significant effect of tag-

ging), we analyzed acorn handling using a two-way mixed model ANOVA, with site (random) and distance (fixed) as the model factors. Although the variances were still heterogeneous after an arcsine transformation (Cochran's C test, $P < 0.05$), ANOVAs are robust to departures from variance assumptions in large experiments where the data are balanced (Underwood 1997). Tukey HSD tests were used for *a posteriori* comparisons between means. *Pseudotsuga* seed handling was analyzed with a two-way mixed model ANOVA, with site (random) and distance (fixed) as the model factors. Variances were determined to be homogenous (Cochran's C test, $P > 0.05$), and Tukey HSD tests were used for *a posteriori* comparisons between means.

RESULTS

The distributions of the *Lithocarpus* and *Pseudotsuga* differed considerably across the ecotone (significant species × distance interaction: $F_{4,40} = 18.123$, $P < 0.001$) (Fig. 3). *Lithocarpus* occurrence was much higher in forest than at the edge or grassland. Conversely, *Pseudotsuga* had much higher occurrence in the grassland and edge than in the forest. Eighty-two and 96% of *Pseudotsuga* seedlings and saplings, respectively, were located at the edge or in the grassland, whereas 80% and 91% of the *Lithocarpus* seedlings and saplings, respectively, were located in the forest.

Lithocarpus acorn densities varied significantly by distance ($F_{4,125} = 6.710$, $P = 0.002$), with no acorns ever found in the far or grassland plots and variable densities among the edge, near forest, and far forest distances across sites (Fig. 4). Acorn densities varied also across the five sites ($F_{4,125} = 3.446$, $P = 0.010$), most likely due to the variation in the number of acorn producing *Lithocarpus* individuals at each site. Because the number of acorns at the edge, near forest, and far forest differed between sites there was also a significant site and distance interaction ($F_{16,125} = 4.299$, $P < 0.001$).

The handling of both *Lithocarpus* acorns and *Pseudotsuga* seeds differed significantly among distances (*Lithocarpus*: $F_{4,80} = 295.030$, $P < 0.001$; *Pseudotsuga*: $F_{4,50} = 35.00$, $P = 0.002$), but not between sites (*Lithocarpus*: $F_{1,80} = 0.765$, $P = 0.384$; *Pseudotsuga*: $F_{1,50} = 0.745$, $P = 0.392$). *Lithocarpus* handling was low at both grassland distances, medium at the edge, and high at both forest distances (Fig. 5). Of all the acorns handled, 59% were eaten, 26% buried, 12% moved, and 3% disappeared. *Pseudotsuga* showed the same general pattern of seed handling, although the edge and far forest were not significantly different, and the near forest had significantly higher handling than all other distances (Tukey HSD tests, $P < 0.05$). There were no significant higher-order interactions for either species.

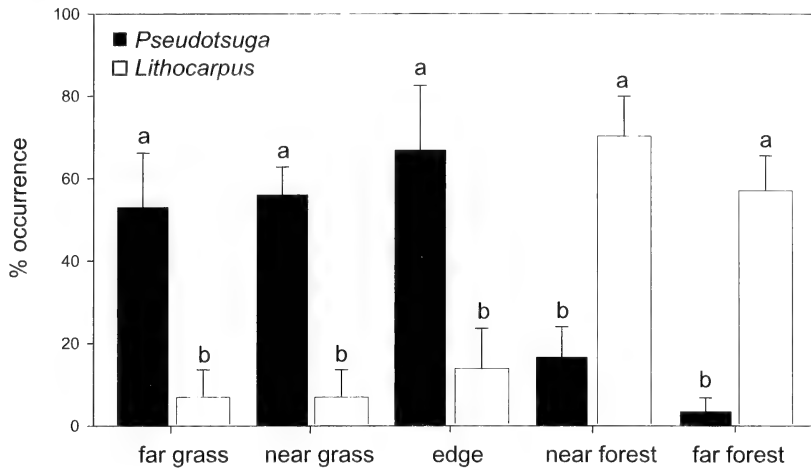


FIG. 3. Mean percent occurrence \pm one standard error of *Lithocarpus* (light bars) and *Pseudotsuga* (dark bars) seedlings and saplings (combined) across the forest-grassland ecotone from five sites. Different letters indicate significant differences (Tukey HSD tests, $P < 0.05$).

DISCUSSION

Based on both the acorn distributions and seed handling experiment, it appears that dispersal limitation is the major factor inhibiting the *Lithocarpus* encroachment. Although we did not directly measure the dispersal of *Pseudotsuga* seeds in this study, there is an abundance of theoretical and empirical research that demonstrate that *Pseudotsuga* seeds are often dispersed over distances greater than *Lithocarpus* (Hermann and Lavender 1990). Most studies of *Pseudotsuga* seed dispersal show declining abundance moving away from forest edges; however, densities can remain relatively high in areas close to forests (see Mair 1973 and citations within). Gashwiler (1969) found that seed abundance was approximately 60% that in the intact forest at 30 m from the forest edge and McDonald (1980) documented an average of 4257 sound seeds/ha up to 60 m from the forest edge. These studies suggest that *Pseudotsuga* seed dispersal into the grassland is quite high, particularly at shorter distances. These dispersal results are also consistent with those predicted by Clark et al. (1999), who modeled the seed dispersal of a number of temperate and tropical tree species and showed that wind-dispersed species were consistently dispersed farther than animal-dispersed species. Compared to the animal-dispersed seed shadows, many wind-dispersed conifer species still had considerable seed shadows at distances ≥ 40 m.

The absence of *Lithocarpus* acorns in the grassland is most likely due to very limited dispersal by small mammals and birds. While some studies demonstrate that animals do transport acorns into grasslands (Darley-Hill and Johnson 1981; Stapanian and Smith 1986; Kollman and Schill 1996), others have shown that dispersers, particularly small mammals, may not frequent areas with less vertical

plant cover (Kikuzawa 1988; Miyaki and Kikuzawa 1988; Quintana-Ascencio et al. 1992; Wada 1993). These movement patterns may differ due to abundances of predators in different habitats (Brown et al. 1999) or simply that animals that spend most of their time in the forest are more likely to eat or disperse food items in the areas where they spend the majority of their time. Despite the fact seed dispersal into the grasslands appeared to be very limited, the seedling and sapling distributions confirm that occasionally *Lithocarpus* acorns are dispersed into the grassland and get established. Therefore, over longer ecological time periods, *Lithocarpus* may show significant encroachment. The lack of correspondence that we observed between the acorn and seedling distributions in the grassland may also be related to the fact that birds remove many acorns before they ever hit the ground (Koenig and Knops 1994). This could have caused us to either over- or underestimate the amount of dispersal into grasslands depending on number of birds that were dispersers versus predators at our sites.

Our results from the seed handling experiment are consistent with those of other studies of acorn predation along forest-grassland ecotones. Stapanian and Smith (1986) found that squirrels cached *Quercus* spp. acorns and *Juglans nigra* L. nuts more often if they were closer to forest edges than in the prairies. In fact, they found that no acorns beyond nine meters into the prairies were ever handled. Hubbard and McPherson (1999) also found lower rates of seed predation in grasslands than adjacent oak woodlands, but handling did occur up to 50 m into the grasslands. In our study, a very small proportion of acorns in the near grassland (5 m) and far grassland (20 m) plots were handled and the handling that did occur may have been caused

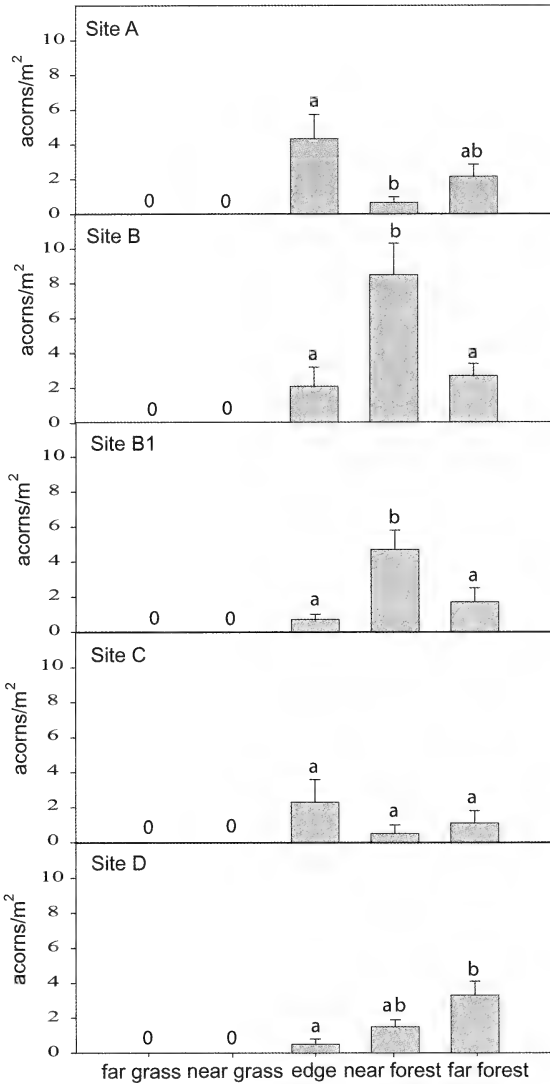


FIG. 4. Mean *Lithocarpus* acorn densities (one standard error) across the forest-grassland ecotone at five sites. Different letters indicate significant differences within each site (Tukey HSD tests, $P < 0.05$).

by gopher activity rather than small mammal predation (the plots with acorns removed had fresh gopher mounds) (Borchert et al. 1989). We are not aware of any other studies that examine *Pseudotsuga* seed handling across a natural forest-grassland ecotone, but Gashwiler (1968) documented that *Pseudotsuga* seed predation in clear-cuts could be quite high. However, Nystrand and Granstrom (2000) found that *Pinus sylvestris* L. seed predation was higher in intact forests than clear-cuts. We believe the effects of *Pseudotsuga* seed handling across the ecotone may be mediated by spatial variation in seed quantity. Although a greater proportion of fallen seeds were handled at the edge than in the grassland, there are likely to be more seeds

present at the edge due to closer proximity to adult trees. As a result, the number of seeds escaping predation in these two habitats may be equivalent, which may explain the equal occurrence of *Pseudotsuga* seedlings and saplings across these distances. In the forest, however, where predation is much higher than at the edge or grassland, seed predators may consume the majority of seeds regardless of the increased seed quantity.

Although seed dispersal and predation may play a significant role in forest encroachment, changing environmental conditions across the forest-grassland ecotone may also affect patterns of establishment. Generally, *Pseudotsuga* establishment and growth is much higher in less shaded environments (Herman and Lavender 1990; Harrington and Tappeiner 1997; Hunter 1997). Because of the low light levels in the forest, its lower seedling and sapling abundances in that habitat may have been driven more by light than seed predation. In contrast, *Lithocarpus* establishment and growth appears to be less sensitive to low light (Harrington and Tappeiner 1997; Hunter 1997). In fact, many oak seedlings actually show better recruitment in shaded than open areas. For example, Callaway (1992) found that the survival of *Quercus douglasii* Hook. & Arn, but not *Q. lobata* Nee, was significantly higher under a shrub canopy than in open grasslands in coastal California. Cruzan (1981) reported the same pattern of increased survival in shaded versus unshaded grassland plots with *Q. agrifolia* and Williams et al. (1991) with *Q. durata* Jepson. In addition to light effects, soil moisture also changes considerably across the forest-grassland ecotone and can be very low in the grassland during the summer months (P. Kennedy unpublished data). Dunne and Parker (1999) documented that first-year *Pseudotsuga* seedling survival in California chaparral, where summer soil moisture consistently dropped to -8.0 MPa, was very low. Little is known about the effects of water stress on *Lithocarpus*, but Harrington et al. (1994) indicated that *Lithocarpus* saplings may be more water stress tolerant than *Pseudotsuga*. Given the importance of these environmental factors in tree seedling establishment and growth, we emphasize the likely potential for forest encroachment to be driven by a series of hierarchical and interactive factors that should not be considered in isolation (House et al. 2003). In addition to this study, we are currently investigating a number of other abiotic and biotic factors affecting forest encroachment on Mount Tamalpais, which will allow us to better determine the specific importance of seed dispersal and predation relative to other factors such as light, soil moisture, herbivory, and mycorrhizal fungi.

In summary, we found that seed dispersal and predation may influence forest encroachment in grasslands, although their effects vary between species. While *Lithocarpus* encroachment into the grassland appeared to be strongly dispersal limited,

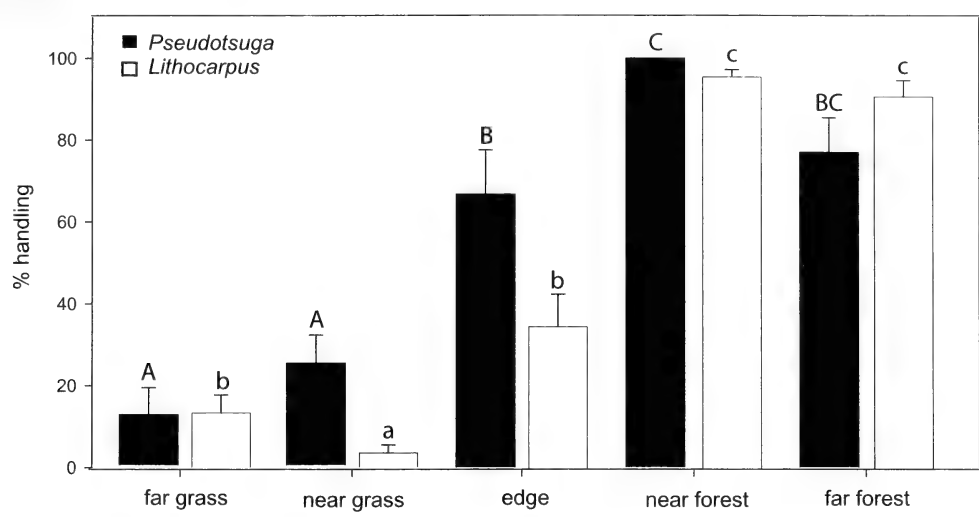


FIG. 5. The mean percent handling \pm one standard error of *Lithocarpus* acorns and *Pseudotsuga* seeds across the forest-grassland ecotone from two sites. See text for definitions of handling. Different letters indicate significant differences (Tukey HSD tests, $P < 0.05$); lower-case letters for *Lithocarpus* and capital letters are for *Pseudotsuga*.

Pseudotsuga encroachment is more likely to be influenced by seed predation than dispersal. Seedling and sapling distributions indicate that *Pseudotsuga* is encroaching into the grassland much more rapidly than *Lithocarpus*, which is most likely due to higher seed dispersal into the grassland combined with relatively low seed predation. However, due to the short-term nature and specific focus of this study, future studies incorporating longer time scales and other factors will better integrate the relative importance of seed dispersal and predation into forest-grassland shifts through time. Specifically, further studies of the ecological factors affecting the survival and growth of subsequent plant life stages of these species are needed to more fully understand the dynamics of forest encroachment in this system.

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POST-DISPERSAL SEED PREDATION VARIES BY HABITAT NOT ACORN SIZE FOR *QUERCUS CHRYSOLEPIS* (FAGACEAE) AND *LITHOCARPUS DENSIFLORA* (FAGACEAE) IN CENTRAL COASTAL CALIFORNIA

PETER G. KENNEDY

Department of Integrative Biology, University of California, Berkeley, CA 94720
pkennedy@socrates.berkeley.edu

ABSTRACT

In this study, I investigated the effects of seed size and habitat on post-dispersal predation of *Quercus chrysolepis* and *Lithocarpus densiflora* acorns in central coastal California. Tagged acorns were located at five distances across two forest-grassland ecotone sites. Although *Q. chrysolepis* acorns were nearly twice as large as those of *L. densiflora*, there was no significant difference in predation between the species or sites. There was, however, a significant difference in acorn predation between habitats, with both species having much higher rates of predation in the forest than in the grassland. While predation occurred across the forest-grassland ecotone, acorn burial only occurred in the forest. These results suggest that habitat had a stronger effect on post-dispersal predation than seed size.

Key Words: forest-grassland ecotone, seed dispersal, seed predation, seed size, *Quercus chrysolepis*, *Lithocarpus densiflora*.

Seed predation can have a large impact on plant distributions and abundances (Crawley 1992). Among the many factors that affect seed predation, the habitat where seeds are located after they are dispersed can play a significant role in determining the amount of predation (Louda 1989). Early work predicted that predation would decline with increasing distance from parent trees (Janzen 1970), and this pattern has been generally confirmed in a range of different habitats (e.g., Cintra 1997; Manson et al. 1998). In addition to variation within habitats, other studies have shown that seed predation may also vary among adjacent habitats (Maron and Simms 1997; Hubbard and McPherson 1999; Nystrand and Granstrom 2000) and at range of spatial (Louda 1982; Sousa and Mitchell 1999) and temporal (Maron and Simms 1997) scales.

A second factor believed to play an important role in seed predation is seed size (Thompson 1987). Theoretically, seeds with larger energy reserves should provide a greater energy return to seed predators and therefore have higher predation than small seeds. While a number of intra-specific and inter-specific studies have documented that larger seeds are consumed more frequently than smaller seeds (Kelrick et al. 1986; Reader 1993; Moegenberg 1996), other work suggests that seed size may not directly affect seed predation (Geritz 1998; Sousa et al. 2003).

Species in the family Fagaceae have been the focus of many post-dispersal predation studies because their typically large seeds are dispersed and consumed by animals (Van der Wall 2001). Rates of seed predation in the genus *Quercus* have been shown to vary across habitats (Kikuzawa 1988; Quintana-Ascencio et al. 1992; Hubbard and McPherson 1999), but no studies have compared how

post-dispersal predation is affected by habitat and seed size. As part of a larger study of the factors affecting woody plant establishment across the forest-grassland ecotone, I investigated the role of seed size and habitat on post-dispersal predation of acorns of *Quercus chrysolepis* Liebm. and *Lithocarpus densiflora* (Hook. & Arn.) Rehder. My specific research objectives were 1) to determine the independent and interactive effects of acorn size and habitat on rates of post-dispersal acorn predation and 2) to better understand how the observed patterns in post-dispersal predation may influence woody plant establishment across forest-grassland ecotones.

METHODS

Study Area

The study was conducted along Bolinas ridge in the Marin Municipal Water District watershed on Mount Tamalpais (37°54'N, 122°37'W) in southern Marin County, CA. The mixed evergreen study forests contain *Pseudotsuga menziesii* (Mirbel) Franco *L. densiflora* (hereafter *Lithocarpus*), *Quercus agrifolia* Nee, *Q. chrysolepis* (hereafter *Quercus*), *Arbutus menziesii* Pursh, *Umbellularia californica* (Hook. & Arn.) Nut., and *Sequoia sempervirens* (D. Don) Endl. (Horton et al. 1999). The grasslands are a mixture of exotic annuals and native and exotic perennials (J. Corbin personal communication). The study area is characterized by a mediterranean climate with seasonal summer dry period and average annual precipitation of 1250 mm (Dunne and Parker 1999).

Quercus and *Lithocarpus* acorns fall most heavily between late September and early November (P. Kennedy personal observation). Both are primarily

small-mammal and bird dispersed (Van der Wall 2001). The western grey squirrel (*Sciurus griseus*) is the primary disperser in the study area, although the Steller's jay (*Cyanocitta stelleri*) may also move acorns (P. Kennedy personal observation). Primary post-dispersal acorn predators include the aforementioned dispersers, acorn woodpeckers (*Melanerpes formicivorus*), mule deer (*Odocoileus Hemionus*), and gophers (*Thomomys* spp.).

Experimental Design

In October 2002, *Quercus* and *Lithocarpus* acorns were collected from a number of trees along Bolinas ridge. The acorns were brought back to the laboratory, immersed in water, and all those still floating after five minutes were considerable inviable and removed (Nyandia and McPherson 1992). Viable acorns were surface sterilized in a 10% bleach solution for five minutes, air dried, and stored at 4°C for a week before tagging. A subset of the acorns of both species was weighed prior to storage ($n = 123/\text{species}$). The acorn tagging method was modified from Forget et al. (1998). A 1-mm diameter hole was drilled through the center of the acorns and threaded with a 1-m piece of fishing line. The line was double-knotted on both sides of the acorn, and a small numbered tag made of orange flagging tape was attached to the opposite end of the line. A pilot study showed that tagging had no effect on seed handling by dispersers/predators (P. Kennedy unpublished data).

Two sites (C and D) separated by approximately 1 km were randomly selected for the seed predation experiment. At both sites, five distances across the forest-grassland ecotone were located: far grassland (20 m into the grassland), near grassland (5 m into the grassland), edge (at the forest-grassland ecotone edge), near forest (5 m into the forest), and far forest (20 m into the forest). At each distance, a 50-m transect running parallel to the forest-grassland ecotone was delineated. Along each transect, 12 one-m² plots, separated by least one m, were randomly established. Each plot was randomly assigned either *Quercus* or *Lithocarpus* acorns ($n = 60$ plots/species). Within each plot, eight acorns were randomly located on the soil surface ($n = 480$ acorns/species: two sites \times five distances \times six plots/distance). The acorns were placed in the plots on October 15. On November 15, the 100-m² area within and around each plot was visually surveyed for ~5 minutes/plot by three people, and the number of acorns and/or tags remaining was recorded.

Statistical Analyses

Acorn weights of *Quercus* and *Lithocarpus* were compared using a Welch's two-sample t-test. An F-test revealed that the variances were heterogeneous; however, the data were normally distributed. To quantify acorn predation, acorns were scored as

"handled" or not. I defined handled as acorns that were eaten, buried, moved, or missing. Although some of the buried, moved, or missing acorns may have escaped predation, the number of moved and missing acorns was low, and many studies have shown that the majority of buried acorns are eventually eaten (see Van der Wall 2001). Therefore, I consider handling to be a maximum estimate of predation. Acorn handling was analyzed using a three-way mixed model ANOVA, with species and distance as fixed factors and site as a random factor. Prior to analysis the data was arcsine transformed to homogenize variances (Cochran's C test, $P > 0.01$). A Tukey HSD test was used for an *a posteriori* comparison between means. Due to low sample sizes and heterogeneous variances, the proportions of acorns eaten and buried were not analyzed statistically.

RESULTS

Acorn size varied significantly between *Quercus* and *Lithocarpus*, with *Quercus* acorns were almost twice as large as those of *Lithocarpus* (*Quercus*: 7.48 ± 0.15 g (mean \pm standard error), *Lithocarpus*: 4.73 ± 0.09 g; $t = 15.13$, $df = 199$, $P < 0.001$). Despite this difference, the amount of acorn handling did not vary significantly between species (species: $F_{1,1} = 3.75$, $P = 0.305$) or sites (site: $F_{1,100} = 0.85$, $P = 0.36$). However, acorn handling did vary across the forest-grassland ecotone (distance: $F_{1,4} = 378.28$, $P < 0.001$). For both species, acorn handling was significantly higher in the forest than the grassland, while the edge experienced intermediate levels of handling (Fig. 1). There were no significant higher-order interactions (species \times site: $F_{1,4} = 2.69$, $P = 0.18$; species \times distance: $F_{4,100} = 0.65$, $P = 0.63$; site \times distance: $F_{1,4} = 2.02$, $P = 0.26$; species \times site \times distance: $F_{4,100} = 0.12$, $P = 0.98$).

For both *Quercus* and *Lithocarpus*, the proportion of acorns eaten in the forest was much higher than in the grassland and intermediate at the edge (Table 1). While there were some acorns eaten in the grassland, no acorns were buried in that habitat. In the forest, *Lithocarpus* had somewhat higher rates of burial than *Quercus*, being highest in the near forest at site D. At all distances, the proportion of acorn eaten was always higher than the proportion buried across species.

DISCUSSION

Although *Quercus* acorns were nearly twice as large as those of *Lithocarpus*, post-dispersal predation did not vary by seed size, but rather by habitat. Both species were consistently handled, eaten, and buried more often in the forest than in the grassland. Patterns of higher acorn predation in forests have been observed in previous studies of *Quercus*. Kikuzawa (1988) found that *Q. mongolica* acorns disappeared fastest from areas with in-

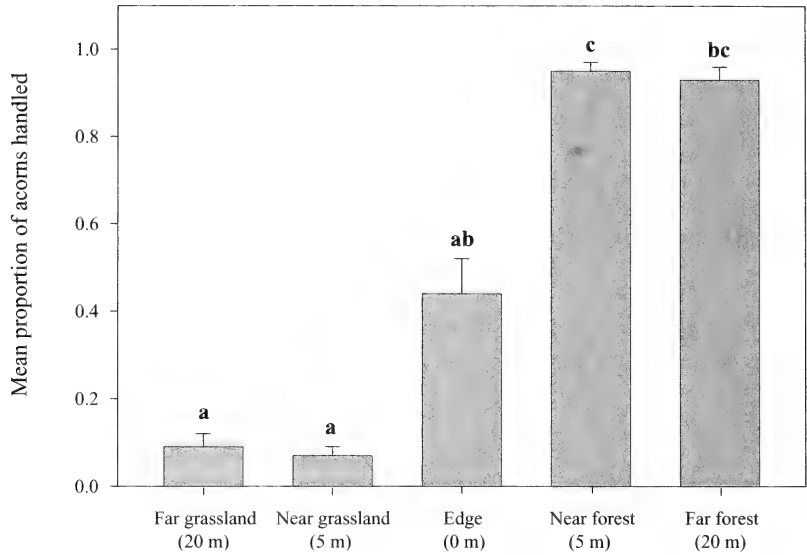


FIG. 1. Mean (\pm one SE) acorn handling of *Quercus chrysolepis* and *Lithocarpus densiflora* across the forest-grassland ecotone on Mt. Tamalpais, CA in 2002. Different letters indicate significant differences among distances ($P = 0.05$). See text for definition of acorn handling.

tact forest canopy and slowest from adjacent bare areas. Similarly, Hubbard and McPherson (1999) documented that predation of *Q. emeryi* acorns was 50% higher under intact canopies than in adjacent grasslands; however, the presence or absence of understory vegetation had no effect on acorn predation in areas with intact canopies. The relatively rapid loss of acorns in the forest (83–96% after one month) was also comparable to rates seen elsewhere. Kikuzawa (1988) showed that after four days all the *Q. mongolica* acorns in unenclosed intact forest locations had been removed. Miyaki and

Kikuzawa (1988) observed the rate of acorn disappearance between fall and winter to be 49% and 99% by the following spring. Similarly, in an eastern U.S. deciduous forest, Sork (1984) found that seed predators consumed greater than 99% of the *Q. rubra* acorns in an eight month period.

While there were a significantly greater number of acorns eaten in the forest than in the grassland, there were also a larger number of acorns buried in the forest as well. Buried acorns often have much higher survival rates than unburied acorns (Borchert et al. 1989; Fuchs et al. 2000), and the absence

TABLE 1. MEAN PROPORTIONS OF ACORNS EATEN AND BURIED ACROSS TWO FOREST-GRASSLAND ECOTONE SITES ON MOUNT TAMALPAIS IN 2002. Standard errors are given in parentheses.

| | Far Grassland (20 m) | Near Grassland (5 m) | Edge (0 m) | Near forest (5 m) | Far forest (20 m) |
|--------------------|----------------------------|----------------------------|---------------|-------------------------|-------------------------|
| Proportion eaten | | | | | |
| <i>Quercus</i> | | | | | |
| Site C | 0 (0) | 0.17 (0.06) | 0.52 (0.18) | 0.94 (0.04) | 0.98 (0.02) |
| Site D | 0.02 (0.02) | 0.02 (0.02) | 0.50 (0.16) | 0.98 (0.02) | 0.98 (0.02) |
| <i>Lithocarpus</i> | | | | | |
| Site C | 0.15 (0.05) | 0.11 (0.05) | 0.44 (0.19) | 0.96 (0.03) | 0.94 (0.04) |
| Site D | 0.13 (0.08) | 0 (0) | 0.31 (0.15) | 0.94 (0.04) | 0.83 (0.11) |
| Proportion buried | | | | | |
| <i>Quercus</i> | | | | | |
| Site C | 0 (0) | 0 (0) | 0 (0) | 0.07 (0.03) | 0.09 (0.05) |
| Site D | 0 (0) | 0 (0) | 0 (0) | 0.13 (0.00) | 0.05 (0.03) |
| <i>Lithocarpus</i> | | | | | |
| Site C | 0 (0) | 0 (0) | 0 (0) | 0.09 (0.04) | 0.23 (0.11) |
| Site D | 0 (0) | 0 (0) | 0 (0) | 0.53 (0.07) | 0.36 (0.09) |

of observed acorn burial in the grassland may limit the rate of successful oak establishment in that habitat. Johnson et al. (1997) found that jays preferentially buried nuts in forest and edge habitats over open grassland habitats; however, others have putatively observed acorn burial by jays in fields (Deen and Hodges 1991). While some studies demonstrate that small mammals do transport acorns into grasslands (Stapanian and Smith 1986; Kollman and Schill 1996), many others have shown that small mammals visit non-forested areas less frequently due to increased risk of mortality by predation (Kikuzawa 1988; Miyaki and Kikuzawa 1988; Quintana-Ascencio et al. 1992; Van der Wall 2001). At both study sites, large raptors were frequently seen flying near the forest-grassland ecotone, which may dissuade small mammals from moving acorns in the grassland.

The reasons why site D had higher proportions of acorn burial than site C and *Lithocarpus* acorns were buried more frequently than those of *Quercus* are less clear. Site D had a slightly more open understory than site C, which may have influenced the dispersers' handling of the acorns. Alternatively, small mammal densities may have varied between sites, which could also have altered handling decisions. Both sites had acorn producing *Lithocarpus* individuals in the canopy, and although they appeared to be qualitatively similar in background acorn density, there may have been slight differences in acorn quantities as well.

Preferences for specific species of seeds have been observed in many small mammal feeding studies (Smith and Follmer 1972; Fox 1982; Jacobs 1992). Lewis (1982) found that squirrel selection of acorns from different species varied according to the energy return of the acorn. The *Quercus* acorns in this study presumably had greater energy return than *Lithocarpus* acorns based on their larger size, which may partially explain their higher proportions of consumption relative to burial at both sites. However, the chemical composition (e.g., tannin levels) of the acorns may also have varied between species, which could have affected the patterns of consumption and burial as well (Smallwood and Peters 1986). One explanation for the relatively high levels of predation of both *Quercus* and *Lithocarpus* may be due to germination strategy. Acorns that do not have a dormant phase are often at least partially consumed immediately by small mammals to decrease acorn loss to seedling germination (Fox 1982). Both Hadj-Chikh et al. (1996) and Smallwood et al. (1998) found that squirrels and other caching animals effectively discriminated between red (which have a dormant phase) and white (which do not have a dormant phase) oak acorns. Since neither *Lithocarpus* nor the *Quercus* species in this study exhibits a dormant phase this may contribute to the high consumption for both species.

In conclusion, I found that habitat plays a more

significant role in post-dispersal acorn predation than seed size. Variation in acorn handling across the forest-grassland ecotone may have important implications for seedling establishment. Very high rates of acorn predation in the forest suggest that seedling recruitment there may be seed limited; however, masting, which is common among oaks and can satiate seed predators, may allow some seedlings to establish regardless of high levels of predation. Furthermore, higher rates of seed burial in the forest will also facilitate greater establishment in that habitat relative to the adjacent grasslands. Post-dispersal acorn predation is clearly affected by a wide range of ecological factors and additional studies are needed to identify other influences controlling this phenomenon. Specifically, studies that determine the chemical composition and nutritional quality of the acorns of both species will help resolve questions about handling decisions. In addition, observational studies of the dispersers will better illuminate the role of habitat in acorn predation. Finally, studies examining a wider range of seed sizes within and between species will provide greater support for the effect of seed size of acorn predation.

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AN INVESTIGATION OF PUTATIVE *TRAGOPOGON MIRUS* (ASTERACEAE) POPULATIONS IN OREGON, USA

STEPHEN C. MEYERS

Genetics Program, Oregon State University, Corvallis, OR 97331-2902
meyersst@science.oregonstate.edu

AARON LISTON

Department of Botany and Plant Pathology, Oregon State University, Corvallis,
OR 97331-2902

ABSTRACT

Tragopogon mirus is a recently formed allotetraploid species, with *Tragopogon dubius* and *Tragopogon porrifolius* as the parental species. A study was conducted on *Tragopogon* populations in Oregon, USA to determine if *T. dubius* and *T. porrifolius* hybridization and subsequent polyploid speciation had occurred. We examined ploidy levels as well as nucleotide data from the chloroplast *trnT-trnL* spacer and nuclear ribosomal ITS regions. While no hybridization or polyploid speciation was found, a seven base pair length mutation found in the chloroplast *trnT-trnL* spacer region should prove useful for determining parentage in populations of *T. mirus*.

Key Words: Oregon, cpDNA, ITS, molecular marker, polyploidy, *Tragopogon mirus*.

Tragopogon L. is an Eurasian genus of 20 species. Three species of this genus, *Tragopogon dubius* Scop., *Tragopogon porrifolius* L., and *Tragopogon pratensis* L. were introduced to North America near the beginning of the twentieth century (Ownbey 1950; Novak et al. 1991). In the late 1940s Marion Ownbey discovered several hybrid, allopolyploid populations of these species in the Palouse region of Washington and Idaho. Ownbey (1950) described and named the allotetraploid species *Tragopogon mirus*, whose parents are *T. dubius* and *T. porrifolius*, and *Tragopogon miscellus*, whose parents are *T. dubius* and *T. pratensis*. In subsequent years more populations of *T. mirus* have been found in the Palouse region (Soltis and Soltis 1991) and Arizona (Brown and Schaak 1972). *Tragopogon mirus* has also been reported in Oregon (Chambers and Sundberg 2000) based on one specimen at the Oregon State University Herbarium (Peck 22380). Studies conducted over the past fifty years suggest at least nine independent origins of *T. mirus* (Ownbey and McCollum 1953, 1954; Brehm and Ownbey 1965; Soltis and Soltis 1989; Novak et al. 1991; Soltis and Soltis 1991; Soltis et al. 1995; Cook et al. 1998).

Our study was motivated by a population of putative *Tragopogon* hybrids, located in the city of Corvallis in the Willamette Valley of western Oregon. The plants of the population, which number approximately 100, resemble *T. porrifolius* except in ligule color. While nearby *T. porrifolius* populations exhibit dark purple ligules, the Corvallis population has light purple ligules, appearing an intermediate color between *T. porrifolius* and yellow-liguled *T. dubius*. Furthermore, the Corvallis

site is a disturbed site with sympatric *T. porrifolius* and *T. dubius* populations.

A study of several allopolyploid *Tragopogon* populations, in the Palouse region (Soltis and Soltis 1989), revealed that the maternal and paternal parent of *T. mirus* were always *T. porrifolius* and *T. dubius*, respectively. The authors of the study attribute this one sided parentage to the fact that, in the Palouse region, *T. dubius* is more common and widespread than *T. porrifolius*. They concluded that pollen load may be an important factor in determining parentage. In ligule color, plants in the Corvallis population differ from known *T. mirus* populations. *Tragopogon mirus* typically has bicolored ligules, with the center yellow and the outer ligules purple. Plants of the Corvallis population have solid, light purple ligules. We postulated that this differing morphology might be due to reversed parentage. In the Willamette Valley *T. porrifolius* is more common and widespread than *T. dubius* (Oregon Flora Project 2004).

In addition to the putative hybrids in Corvallis, we examined two herbarium specimens from north-eastern Oregon: *Stevenson s.n.* (ORE) which matched plants of the Corvallis population in ligule color and the putative *T. mirus*, Peck 22380 (WIL-LU), reported by Chambers and Sundberg (2000) (Table 1).

To evaluate hybridization and parentage we sequenced both the plastid *trnT-trnL* spacer and nuclear ribosomal ITS regions. Ploidy levels were measured using chromosome counts and flow cytometry.

MATERIALS AND METHODS

DNA was obtained from fresh plant material, dried herbarium specimens and cotyledons germi-

TABLE 1. COLLECTION DATA AND PLANT MATERIAL USED FOR DNA EXTRACTIONS AND SUBSEQUENT DETERMINATIONS OF PUTATIVE HYBRID SPECIMENS.

| Sample | Collection data (all locations in Oregon) | DNA obtained from | Determination from DNA data |
|-----------------------------|--|----------------------|--------------------------------|
| Known <i>T. dubius</i> | | | |
| D1 | Benton Co., Corvallis, <i>Schenk 118-1</i> (OSC) | fresh leaf | |
| D2 | Benton Co., Corvallis, <i>Schenk 118-2</i> (OSC) | fresh leaf | |
| Known <i>T. porrifolius</i> | | | |
| P1 | Benton Co., Corvallis, <i>Meyers 112</i> (OSC) | fresh leaf | |
| P2 | Benton Co., Corvallis, <i>Meyers 113</i> (OSC) | fresh leaf | |
| Putative hybrids | | | |
| M1 | Benton Co., Corvallis, <i>Meyers 111</i> (OSC) | fresh leaf | <i>T. porrifolius</i> |
| MC | Benton Co., Corvallis, <i>Halse 5890</i> (OSC) | seed | <i>T. porrifolius</i> |
| ORE | Union Co., near La Grande, <i>Stevenson s.n.</i> (ORE) | dried leaf | <i>T. porrifolius</i> |
| WILLU | Union Co., near Elgin, <i>Peck 22380</i> (WILLU) | dried leaf | <i>T. dubius</i> |

nated from seed (Table 1). Approximately 50 mg of plant material was used to extract DNA using a DNeasy Plant Mini kit (Qiagen, Valencia, CA). Polymerase chain reactions for plasmid DNA were performed in 20 µl reactions volumes which contained, 3.0 mM MgCl₂ (Promega, Madison, WI), 10X Promega Buffer A, 0.1 µM each dATP, dCTP, dGTP and dTTP (Epicentre, Madison, WI), 10 pmol of each primer (Taberlet et al. 1991), 1X BSA, 1 unit of *Taq* polymerase (Promega), and 2.0 µl DNA template. ITS reactions were conducted using the same amount and concentration of reactants with the following exceptions: 5% dimethylsulfoxide (DMSO) and 10 pmol each primer (Liston et al. 1996). The reactions, overlaid with approximately 10 µl of mineral oil, were placed in an MJ research programmable thermal controller programmed as follows: 5 min at 95°C, 25 cycles of 1 min at 95°C, 4 min at 65°C, with a 10 min final extension at 65°C. Following PCR, products were purified using a QIAquick PCR purification kit (Qiagen, Valencia, CA). As a result of low DNA yields the 50 µl elutions were concentrated to 5 µl using a LABCONCO centrivap-concentrator. DNA sequences were obtained using an ABI 373A DNA sequencer (Applied Biosystems, Foster City, CA). Sequences were aligned and analyzed using BioEdit for Windows 95/98/NT (Hall 1999).

Chromosome counts were performed on putative hybrids grown from seeds collected at the Corvallis site, using a modified procedure described by Rivera-Lizarazu et al. (1996). Root tips were collected in the morning (10:30 a.m.) and placed in a flask with a pre-treatment solution of 0.5 g liter⁻¹ colchicine, 25 g liter⁻¹ 8-hydroxyquinoline, and 1.5% (v/v) DMSO for 3.5 h at room temperature in the dark. Root tips were transferred to a solution of 2% (w/v) aceto orcein solution and stored in a refrigerator for 48 h. Root tips were squashed in 45% acetic acid and the chromosomes counted.

Flow cytometry was performed on putative hybrid cotyledons grown from seeds collected at the

Corvallis site using a Partec GmbH ploidy analyzer (Partec, Münster, Germany).

RESULTS

The chromosome counts of putative hybrids, grown from seed collected at the Corvallis site, revealed a chromosome number of 2n=12. To confirm the chromosome counts we compared the ploidy level of several other putative hybrids with the known ploidy level of *T. dubius* and *T. porrifolius* (2n=12) using flow cytometry. On the cytometer, the putative hybrids produced peaks in the same channel as *T. dubius* and *T. porrifolius*. From these results, we conclude the plants in the Corvallis population are diploid.

To explore the possibility of hybridization we examined sequence data of the chloroplast *trnT-trnL* spacer and nuclear ribosomal ITS regions. Upon alignment, *trnT-trnL* sequences of *T. porrifolius* and *T. dubius* populations revealed three base pair changes and a seven base pair length mutation (GenBank acc. nos. AY525374, AY525375). The ITS sequences revealed seven base pair changes (GenBank acc. nos. AY525376, AY525377). These distinct sequences were compared with those of the putative hybrids. The sequences of three putative hybrids, including the Corvallis population, were found to match the sequences of *T. porrifolius*, while sequences of the herbarium specimen from Elgin (*Peck 22380*) were found to match sequences of *T. dubius* (Table 1).

DISCUSSION

The seven base pair length mutation in the plastid *trnT-trnL* spacer region clearly distinguishes the chloroplast genomes of *T. dubius* and *T. porrifolius* and can be easily scored on an agarose gel. The chloroplast genome is maternally inherited in most angiosperms, including members of the Asteraceae (Sears 1980; Whately 1982; Corriveau and Coleman 1988). Further, cytological and cpDNA studies suggest that the chloroplast genome is maternally

inherited in *Tragopogon* (Ownbey and McCollum 1953; Soltis and Soltis 1989). In ongoing and future studies, the seven base pair length mutation should provide an effective marker to determine parentage in populations of *T. mirus*.

Chromosome counts and flow cytometry confirm that plants at the Corvallis site are diploid, and not tetraploid, as in *T. mirus*. In addition, DNA sequences confirm that the Corvallis plants and the herbarium specimens analyzed are *T. porrifolius*. The result of this study is that no Oregon records of *T. mirus* were found, including the specimen cited by Chambers and Sundberg (2000). We conclude the light colored ligules of the plants and specimens we analyzed are not the result of a hybridization event between *T. dubius* and *T. porrifolius*, but rather a morphological variant of typical *T. porrifolius*.

Despite sympatric populations of *T. dubius* and *T. porrifolius*, hybridization and subsequent allopolyploid speciation of *T. mirus* has yet to be recorded in Oregon. One difference between the Palouse region of Washington and Idaho, where *T. mirus* is commonly found, and the Willamette Valley, is the asymmetric abundance of *T. dubius* and *T. porrifolius*. In the Palouse region, *T. dubius* is more common than *T. porrifolius*, while in the Willamette Valley the respective abundance is opposite. Given that *T. dubius* has always been found to be the paternal parent of *T. mirus* in the Palouse region (Soltis and Soltis 1989), the lesser abundance of *T. dubius* in the Willamette Valley, and resulting lower pollen contribution, may explain the absence of *T. mirus* in western Oregon. In northeastern Oregon, *T. dubius* is abundant while *T. porrifolius* is very rare and only known from the vicinity of La Grande (Oregon Flora Project 2004). Although the two examined herbarium specimens were determined to not represent *T. mirus*, field studies are needed to confirm the absence of this hybrid species in the region.

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SMALL-SCALE COMMUNITY ANALYSES OF ALPINE RIDGE VEGETATION IN THE CENTRAL SIERRA NEVADA

SUSAN E. ELLIOTT¹ AND ERIK S. JULES

Department of Biological Sciences, Humboldt State University, Arcata, CA 95521

ABSTRACT

Most studies of alpine vegetation communities focus on the variation occurring across large scales, in which diverse environmental habitats are assessed across the landscape and detailed plant associations are described. However, community patterns occurring at more intricate scales are easily concealed by such a broad perspective. To complement large-scale studies, we assessed smaller-scale patterns occurring at the extremes of moisture and exposure gradients in an alpine environment. We studied the variation in plant community composition among and within seven ridges extending down two rocky metamorphic peaks in Yosemite National Park. Species cover and environmental factors (proximity to a summit, elevation, aspect, slope, and substrate size) were sampled in 281 2 × 2-meter plots. Variation among ridges was primarily determined by differences in aspect. Within the ridges, although the physical environment in which we sampled was seemingly homogenous, ordinations identified two distinct vegetation types: (1) high diversity and high cover vegetation (HD), dominated by cushion plants and (2) low diversity and low cover vegetation (LD), dominated by plants in large clumps or small rosettes. In general, LD vegetation was found nearer to the summit and was highly variable in its component species, while HD vegetation was found farther along the ridgeline and was relatively uniform. This non-intuitive pattern in which cushion plants do not dominate the most exposed habitat occurred independent of elevation. Instead, our data suggest that along with changes in rock size and aspect, proximity to a summit is a meaningful factor governing alpine community structure. We discuss the water limited conditions imposed by the absence of smaller rock structure at the summit and how this may allow for only the sparse LD vegetation to persist there.

Key Words: alpine plant communities, environmental gradients, ordination, scale, Yosemite National Park, Sierra Nevada.

Alpine plant communities have been analyzed and classified for decades with studies that usually operate across broad geographic scales and include diverse habitats (e.g., Douglas and Bliss 1977; Kirkpatrick and Bridle 1998; Wiser 1998). These studies often (1) establish broad inventories of co-occurring alpine plant species and (2) identify primary environmental factors that control these patterns (e.g., Taylor 1984; Urbanczyk and Henderson 1994). The resulting alpine vegetation patterns have consisted of well-defined groups of species, which are governed primarily by moisture availability (e.g., Major and Taylor 1988). Moisture availability has been assessed using surrogate factors such as aspect, exposure, and temperature to assess vegetation patterns (Mark et al. 2000). However, it is unclear whether or not these factors carry the same importance at finer scales.

Patterns at different scales often elucidate different ecological processes (Turner 1989). However, only fairly recently has this question of scale begun to be evaluated and applied to alpine vegetation studies (Kirkpatrick and Bridle 1998; Mark et al. 2000). One study from the North Carolina piedmont confirms that examining patterns at a smaller

scale can be useful in detecting locally important processes, which would normally be masked by more widely varying factors in large-scale studies (Reed et al. 1993). In addition, Mohler (1983), in a theoretical simulation study, showed that intense sampling at gradient extremes produces more accurate autecological species descriptions. Along with distinguishing patterns that may be related to local ecological processes, appropriately-scaled alpine community analyses can provide important baseline data for monitoring and predicting future vegetation dynamics that may result from climate changes (Gottfried et al. 1998; Mark et al. 2000).

Our study uses a classical community ordination approach with a contemporary consideration of scale to analyze alpine vegetation in the central Sierra Nevada. We chose a relatively homogenous habitat (rocky metamorphic ridges), to limit overpowering patterns originating from extensive variation in moisture and exposure, which are often primary factors involved in governing alpine plant communities. Ridges represent an extreme xeric environment because of their broad contact with drying winds and intense solar radiation (Billings 2000). This is especially true in the Sierra Nevada, where much of the alpine flora is more closely related to adjacent eastern high desert species rather than traditional arctic-alpine taxa (Chabot and Billings 1972; Major and Taylor 1988). Because of the

¹ Current address: Department of Biological Sciences, Dartmouth College, Hanover NH 03755. e-mail: Susan.E.Elliott@dartmouth.edu

TABLE 1. GENERAL CHARACTERISTICS FOR THE SEVEN RIDGES EXTENDING OFF OF MT. DANA AND MT. GIBBS, YOSEMITE NATIONAL PARK. Numbers in parentheses represent the percentage of the total plots sampled on that ridge that contained vegetation.

| Peak | Ridge | Elevation range (m) | Aspect | Length (m) | Total plots | Vegetated plots |
|------------|-------|------------------------|--------|---------------|----------------|--------------------|
| Dana | 1 | 3980–3360 | NW | 1120 | 56 | 43 (77%) |
| Dana | 2 | 3980–3785 | E | 480 | 24 | 9 (38%) |
| Dana | 3 | 3785–3755 | NE | 520 | 26 | 20 (78%) |
| Gibbs | 4 | 3890–3600 | WNW | 960 | 48 | 37 (77%) |
| Gibbs | 5 | 3890–3700 | ESE | 640 | 32 | 25 (78%) |
| Gibbs | 6 | 3890–3765 | NNE | 760 | 38 | 18 (47%) |
| Gibbs | 7 | 3890–3655 | SW | 1140 | 57 | 47 (82%) |
| All ridges | | | | | 281 | 199 (71%) |

almost desert-like habitat found on ridges, our samples were effectively taken at the extreme end of a montane moisture gradient. In addition, aspect could be an important factor determining plant communities at high altitudes (Pinder et al. 1997). However, on high altitude ridges, we predicted that the degree to which aspect would govern community composition would be minimal because all ridges are exposed to sun and precipitation to a similar degree, unlike their adjacent slopes. In addition to receiving similar exposure, the substrate on our study ridges was overwhelmingly composed of large metamorphic rocks, which have the tendency to break into small irregular fragments, allowing for very minimal moisture retention (Taylor 1984). Since different substrates often harbor very different plant communities (Johnson and Billings 1962; Bamberg and Major 1968), we hoped that minimizing the variation in different rock types might reveal more subtle patterns in the vegetation.

The primary objectives of our study were to describe the rocky alpine ridge-top vegetation patterns occurring at small scales and to relate these patterns to variation in the physical environment. Specifically, we sought to describe the variation in species composition and abundance among and within the ridges. By relating these patterns to measured abiotic variables (i.e., proximity to a summit, elevation, aspect, slope, and rock size), we hoped to discern the primary environmental factors controlling plant composition and abundance in this relatively homogenous habitat. Finally, we wished to examine how the vegetative patterns and governing factors in our small-scale study compared with those identified in larger-scale studies.

METHODS

Study Areas

The two peaks we studied (Mt. Dana and Mt. Gibbs) are located in the central Sierra Nevada on the border between the Yosemite Wilderness and the Ansel Adams Wilderness in Mono County, California. Mt. Dana (3983 m; 37°57'59"N, 119°13'13"W) has two distinct ridges, one of which we divided and analyzed as two different ridges

because the second half takes a distinct jagged turn, separating it from the first part of the ridge. Mt. Gibbs (3890 m; 37°52'38"N, 119°12'40"W) has four distinct ridges extending off its summit. The substrate on both peaks is metamorphic in origin. The climate in this region consists of long cold winters, short dry summers, and frequent strong winds. This creates an environment where plants must tolerate low temperature extremes, periodic heat stress, and high rates of evapotranspiration (Körner 2003).

Data Collection

The data for this study were collected in July and August of 2001 while biomass production was at its peak. This particular summer was relatively dry, so species abundances should be considered only as a relative description of what can be found on these ridges.

The study included seven ridges, each containing 24–57 sampling plots (Table 1). Sampling for each ridge began at the summit and moved down the ridge. The plots were located in a line that was defined as the highest point along the ridge. Thus, the line was able to curve with the ridge as it descended downward at various aspects. Plots were each 2 × 2 meters and were placed at random distances between 15 and 25 meters apart, down the length of the ridge. We stopped sampling when the defining apex of the ridge was no longer apparent. This point was reached when the angle of the slopes descending off each side of the ridge were roughly horizontal.

At each plot, we measured distance from the summit, elevation, aspect, slope, species composition, and rock size composition. Each plot was divided into four 1 × 1-meter subplots. In each subplot, vegetation and substrate were classified and quantified using standard relevé techniques. Each distinct clump of vegetation was classified into one of five size classes based on the clump's basal diameter: 1–2.5 cm, 2.5–5 cm, 5–10 cm, 10–20 cm, and 20–30 cm. For each species in the plot, we recorded its frequency at each size class. These were transformed into percent cover values by dividing total basal area by plot area. We estimated

that each clump was roughly a circle and used the median diameter for each size class to calculate the basal area covered by each size class. To determine rock size composition we visually estimated the percent cover of rocks of different diameters: soil-1 cm, 1–5 cm, 5–30 cm, 30–60 cm, and >60 cm. The “major substrate size” was defined as the size class taking up the greatest proportion of the plot. We identified plant species in the field or in the Yosemite National Park research station in Tuolumne Meadows, using Hickman (1993), Weeden (1996), and Botti (2001).

Data Analysis

We preformed Bray-Curtis ordinations with the software PC-Ord 4.0 (McCune and Mefford 1999) to assess patterns in vegetation composition. To avoid effects that can result from rare occurrences, we included only those species that were found in >5% of the plots. We transformed our data with Beal's smoothing function, a robust technique used to blend information from a large number of small sample units, where many species have minimal cover (McCune 1994). Using the ordination solution on two axes, we used both Pearson correlations and linear regressions to analyze relationships among environmental factors and species composition. Finally, we used Multi-Response Permutation Procedures (MRPP) in PC-Ord 4.0 (McCune and Mefford 1999) to evaluate differences in composition between ridges.

RESULTS

We found a total of 36 plant species, 19 of which occurred in >5% of the plots (Table 2). Although individual species were found in up to 50% of the vegetated plots on an individual ridge, vegetation was very sparse; 30% of the 281 plots sampled were completely void of vegetation (Tables 1 and 2). Individual ridges contained between 8 and 24 species (Table 2). Of the vegetated plots, mean richness per ridge ranged from 1.9 to 5.9 species. This variation in richness was not significantly correlated with ridge length (effective sample area) ($R^2 = 0.396$, $P = 0.130$). Thus, species richness was affected by some other factor besides sample area.

Variation Among Ridges

Species composition and abundance varied among ridges. MRPP showed that nearly all ridges were significantly different from one another in their species composition (Table 3). The only non-significantly different pairs of ridges were 4–6 and 5–6 ($P = 0.09$ and $P = 0.27$). This variation may largely be an artifact of the differences in aspect among ridges. For example, Figure 1 shows vertical separation among different ridges along Axis 2. The ridges toward the top of the ordination are facing between NW and E (which includes Ridges 1, 2, 3, and 6; Fig. 1 and Table 1). Plots on the lower

side of the ordination are mostly dominated by Ridges 4, 5, and 7, with ESE to WNW aspects (Fig. 1, Table 1). Ridge 7 (Gibbs) was especially divergent from ridges 1, 2, and 3 (Dana) ($P = 0.003$, 0.00003, and $< 1.0 \times 10^{-6}$, respectively). Finally, vertical separation among plots was also related to the abundance of *Calyptridium umbellatum* and the amount of small (1–5 cm) rocks. As the amount of small rocks increased, so did *C. umbellatum* cover ($R^2 = 0.443$, $P < 0.001$).

Variation Within Ridges

Patterns of species composition and abundance also varied within ridges. Ordination analyses revealed that plots were distributed along a somewhat linear continuum (Fig. 1); most of the variation in species composition was explained by Axis 1 (first eigenvalue $R^2 = 0.836$). On the left side of the ordination, vegetation was characterized by high cover, high species richness, and an abundance of cushion plants (hereafter HD = high diversity vegetation; Table 4). For example, the occurrence of plants such as *Podistera nevadensis*, *Phlox pulvinata*, *Astragalus kentrophyta* var. *danaus*, and *Eriogonum ovalifolium* var. *nivale* had a strong negative correlation with Axis 1 (Table 4). The high cover of these dominant plant species increased the tightness of their clustering since the ordination takes into consideration both composition and abundance. These mat-forming species were joined by fine upright graminoids such as *Poa stebbinsii*, *Trisetum spicatum*, and *Festuca brachyphylla* subsp. *breviculmis*. On the right side of the ordination, vegetation was characterized by low cover, low species richness, robust upright plants, and occasionally by sparse minute plants (hereafter LD = low diversity vegetation; Table 4). Instead of plots with rich clustered mats, plots on the right side of the spectrum often contained solitary patches of single or relatively few associated species. These species, such as *Polemonium eximium*, robust *Carex* species, and *Hulsea algida*, have greater above-ground biomass than the HD cushion species, even though they may provide less total cover (basal area). Plots with LD vegetation also may contain smaller species such as *Muhlenbergia filiformis*, *Draba breweri*, and mosses.

The distinction between HD and LD vegetation is related to the distance plots were located from the summit, which was negatively correlated with Axis 1 (Table 4). Richness and vegetative cover were positively correlated with plot distance from the summit (richness: $R^2 = 0.186$, $P < 0.001$, vegetative cover: $R^2 = 0.144$, $P < 0.001$). While LD vegetation was common within 200 m of the summit, HD vegetation extended down the length of the ridge (Fig. 2). However, as in most systems, the involved species were not strictly partitioned. For example, while *Carex* species were most common near the summit, they were also found farther down

TABLE 2. LIST OF SPECIES FOUND, WITH SPECIES CODES AND FREQUENCIES OF OCCURRENCE ON EACH RIDGE. Bolded species were found in greater than five percent of the plots.

| Code | Species | Frequency | | | | | | |
|-------|--|-----------|----|----|-------|----|----|----|
| | | Dana | | | Gibbs | | | |
| | | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
| ANME | <i>Antennaria media</i> E. Greene | 3 | 0 | 0 | 0 | 1 | 0 | 1 |
| ANSE | <i>Androsace septentrionalis</i> L. subsp. <i>subumbellata</i> G. Robb. | 4 | 0 | 0 | 0 | 0 | 0 | 0 |
| ARLE | <i>Arabis lemmonii</i> S. Watson | 1 | 0 | 2 | 0 | 0 | 0 | 0 |
| ASKE | <i>Astragalus kentrophyta</i> (A. Gray var. <i>danaus</i> (Barneby) Barneby | 19 | 0 | 3 | 4 | 2 | 0 | 2 |
| CAHE | <i>Carex heteroneura</i> W. Boott var. <i>heteroneura</i> | 10 | 3 | 13 | 10 | 5 | 3 | 2 |
| CALE | <i>Carex leporinella</i> Mackenzie | 5 | 0 | 10 | 2 | 11 | 7 | 7 |
| CANA | <i>Castilleja nana</i> Eastw. | 4 | 0 | 2 | 0 | 0 | 0 | 1 |
| CARO | <i>Carex rossii</i> Boott | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| CAUM | <i>Calyptidium umbellatum</i> (Torrey) E. Greene | 0 | 0 | 0 | 9 | 2 | 3 | 10 |
| CAVE | <i>Carex vernacula</i> L. Bailey | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| DRBR | <i>Draba breweri</i> S. Watson | 17 | 3 | 3 | 0 | 2 | 2 | 6 |
| DRLE | <i>Draba lemmonii</i> S. Watson | 2 | 0 | 1 | 0 | 0 | 0 | 0 |
| ERCO | <i>Erigeron compositus</i> Pursh | 24 | 1 | 2 | 5 | 6 | 8 | 3 |
| ERDI | <i>Ericameria discoidea</i> (Nutt.) G. Nesom | 0 | 0 | 0 | 1 | 0 | 0 | 11 |
| ERIN | <i>Eriogonum incanum</i> Torrey & A. Gray | 11 | 0 | 3 | 3 | 2 | 0 | 15 |
| EROV | <i>Eriogonum ovalifolium</i> Nutt. var. <i>nivale</i> (Canby) M. E. Jones | 5 | 0 | 0 | 3 | 0 | 0 | 3 |
| ERVA | <i>Erigeron vagus</i> Payson | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| FEBR | <i>Festuca brachyphylla</i> Schultes & Schultes subsp. <i>breviculmis</i> S. Frederiksen | 22 | 0 | 7 | 13 | 10 | 6 | 18 |
| HECO | <i>Hesperostipa comata</i> (Trin. & Rupr.) Barkworth subsp. <i>comata</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| HUAL | <i>Hulsea algida</i> A. Gray | 2 | 0 | 4 | 0 | 1 | 3 | 0 |
| IVLY | <i>Ivesia lycopodioides</i> A. Gray subsp. <i>lycopodioides</i> | 2 | 0 | 2 | 0 | 0 | 0 | 1 |
| JU1 | <i>Juncus</i> sp. 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 |
| JU2 | <i>Juncus</i> sp. 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| MOSS | acrocarpous moss species | 15 | 6 | 10 | 4 | 3 | 2 | 3 |
| MUFI | <i>Muhlebergia filiformis</i> (Thurber) Rydb. | 8 | 1 | 0 | 0 | 0 | 0 | 1 |
| OXDI | <i>Oxyria digyna</i> (L.) Hill | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| Penst | <i>Penstemon</i> sp. | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| PHDI | <i>Phlox pulvinata</i> (Wherry) Chronq. | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| PHPU | <i>Phlox diffusa</i> Benth. | 25 | 0 | 5 | 8 | 11 | 5 | 26 |
| POEX | <i>Polemonium eximium</i> E. Greene | 5 | 1 | 1 | 7 | 0 | 0 | 0 |
| PONE | <i>Podistera nevadensis</i> (A. Gray) S. Watson | 18 | 1 | 2 | 9 | 10 | 3 | 21 |
| POPS | <i>Potentilla pseudosericea</i> Rydb. | 5 | 0 | 0 | 0 | 0 | 0 | 0 |
| POST | <i>Poa stebbinsii</i> R. Soreng | 18 | 0 | 7 | 7 | 7 | 1 | 19 |
| RASC | <i>Raillardella scaposa</i> (A. Gray) A. Gray | 0 | 0 | 0 | 0 | 0 | 0 | 7 |
| TOSC | <i>Townsendia scapigera</i> Eaton | 0 | 0 | 5 | 10 | 7 | 0 | 24 |
| TRSP | <i>Trisetum spicatum</i> (L.) Richter | 24 | 0 | 4 | 22 | 16 | 5 | 42 |
| | Total Plots with Vegetation | 43 | 9 | 20 | 37 | 25 | 18 | 47 |
| | Total Plots without Vegetation | 13 | 15 | 6 | 11 | 7 | 20 | 10 |
| | Total Species Richness | 27 | 8 | 20 | 16 | 16 | 12 | 24 |
| | Average Species Richness per Plot | 6 | 2 | 4 | 3 | 4 | 3 | 5 |

the ridge (Fig. 2). Similarly, *Podistera nevadensis* was characteristic of HD vegetation, but was also found within 200 m of the summit (Fig. 2). While these two species ranged along the entire ridges, when found near the summit, they occurred in plots with low richness and low cover. Plots with these species farther down the ridge had high richness and high cover. Thus, the community characteristics of richness and cover, rather than particular species identities, gave more consistent descriptions of the patterns identified by the ordination analyses. Rock size also varied with the distance from the summit. Rocks in the two smaller size classes (soil-1 cm and 1–5 cm) increased farther down the ridge ($R^2 = 0.036$, $P = 0.0014$ and $R^2 = 0.027$, $P =$

0.0063, respectively). Distance from the summit was not confounded by elevation. Elevation varied little among plots (Table 1) and showed little to no correlation with either ordination axis (Table 4).

DISCUSSION

In general, the individual species we identified on the ridges that extend off of Mt. Dana and Mt. Gibbs were similar to those found in detailed surveys of alpine vegetation from Yosemite National Park (Pemble 1970; Taylor 1984). While studies such as these describe xeric ridge species collectively as one general vegetation type, our study further partitioned that one type by evaluating the pat-

TABLE 3. RESULTS FROM THE MULTI-RESPONSE PERMUTATION PROCEDURES TESTING FOR DIFFERENCES IN SPECIES COMPOSITION AMONG RIDGES AND PEAKS. Test-statistic values (T) and significance levels (* P < 0.05, *** P < 0.001) are shown for differences (A) between individual ridges, (B) among groups of ridges, and (C) between peaks.

| | 2 | 3 | 4 | 5 | 6 | 7 |
|------------|----------|-----------|---------|----------|----------|----------|
| A. | | | | | | |
| 1 | -5.71* | -0.962*** | -5.037* | -2.82* | -2.86* | -16.1*** |
| 2 | | -2.37* | -4.73* | -8.19*** | 4.23* | -21.1*** |
| 3 | | | -4.32* | -7.51*** | -3.29* | -22.6*** |
| 4 | | | | -2.32* | -1.12ns | -9.97*** |
| 5 | | | | | -0.606ns | -3.57* |
| 6 | | | | | | -11.2*** |
| B. | | | | | | |
| 1, 2, 3 | -9.23*** | | | | | |
| 4, 5, 6, 7 | -8.43*** | | | | | |
| C. | | | | | | |
| Dana-Gibbs | -13.5*** | | | | | |

terns at a finer scale. We found that there was not only variation among ridges of this same habitat type but also within each ridge. In contrast with large-scale analyses that characterize vegetation types based on common member species, the patterns we found within ridges were more readily described by variation in richness and cover.

Variation Among Ridges

Surprisingly, we found that variation among ridges was most strongly controlled by aspect. Regardless of aspect, all ridges are overwhelmingly exposed to wind and sun. Thus, we assumed that aspect would have little bearing on micro-climatic conditions along ridges. Nevertheless, aspect may

indeed help explain the significant compositional differences among the ridges confirmed by the MRPP analyses as it has in large-scale alpine studies (Mark et al. 2000; Glew 1994). Overall, the ridges varied little in most of the abiotic factors we measured, except for differences in aspect (Table 1). Changes in aspect can be accompanied by changes in moisture availability, solar radiation, wind, and snow-pack, all of which contribute to alpine plant community composition at large scales (Pinder et al. 1997). Since we did not measure these specific variables, aspect may still have served as a representation for changes in the combinations of these three factors.

We hypothesize that additional differences may

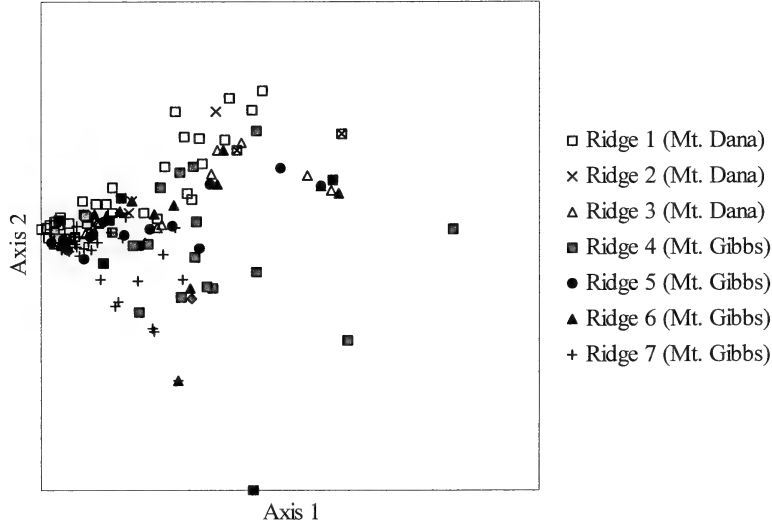


FIG. 1. Results of a Bray-Curtis ordination showing patterns for seven ridges on Mt. Dana (1–3) and Mt. Gibbs (4–7), Yosemite National Park. Plots do not cluster into distinct groups based on species composition. Instead, correlations along Axis 1 (explaining 83.6% of the variation) correspond to community characteristics of richness and total vegetative cover (see Table 4). In the loosely clustered plots, vertical variation is roughly separated by different ridge identity.

TABLE 4. CORRELATION VALUES FOR SPECIES (GIVEN BY CODE) AND ENVIRONMENTAL FACTORS WITH ORDINATION AXES.

| Species | | | Environmental Factors, Richness, and Cover | | |
|---------|--------|--------|--|--------|--------|
| | Axis 1 | Axis 2 | | Axis 1 | Axis 2 |
| PONE | -0.939 | -0.054 | Species Richness | -0.522 | 0.11 |
| PHPU | -0.922 | 0.039 | Total Vegetative Cover | -0.447 | 0.051 |
| POST | -0.904 | -0.015 | Distance from Summit | -0.366 | 0.124 |
| TRSP | -0.904 | -0.407 | Elevation | -0.009 | 0.007 |
| ASKE | -0.894 | 0.083 | Major Substrate Size | 0.012 | 0.083 |
| EROV | -0.826 | -0.099 | 5–30 cm | 0.027 | -0.277 |
| FEBR | -0.707 | 0.449 | 30–60 cm | 0.039 | 0.315 |
| ERCO | -0.601 | 0.302 | 1–5 cm | 0.11 | -0.507 |
| ERIN | -0.576 | -0.351 | >60 cm | 0.138 | 0.238 |
| TOSC | -0.573 | -0.486 | Slope | 0.165 | 0.351 |
| DRBR | -0.274 | 0.389 | soil-1 cm | 0.222 | 0.242 |
| ERVA | 0.041 | 0.253 | Aspect | 0.291 | 0.286 |
| POEX | 0.165 | 0.344 | | | |
| CAUM | 0.196 | -0.838 | | | |
| CALE | 0.306 | 0.285 | | | |
| MOSS | 0.424 | 0.465 | | | |
| HUAL | 0.435 | 0.326 | | | |
| MUFI | 0.503 | 0.524 | | | |
| CAHE | 0.947 | 0.225 | | | |

also be attributed to the micro-topography of the surface rocks and the sub-surface rock architecture on different ridges. *Calyptidium umbellatum*, for example, was tightly correlated with one particular rock size (1–5 cm). The prevalence of smaller rock sizes decreased toward the summit. The eco-physiological effect of different rock sizes may be related to the plant’s ability to penetrate into a moisture supply, its ability to establish in an area relatively free of organic matter or soil, and the shelter it receives by large rocks (Körner 2003).

Variation Within Ridges

Both community characteristics (richness and cover) as well as individual species present varied along the length of each ridge. The strongest environmental factor correlated with these patterns was proximity to the summit (i.e., HD vegetation was farther from the summit than LD vegetation;

Table 4 and Fig. 2). Wind in exposed alpine areas can limit plant growth (and indirectly plant distributions) by increasing evaporation and reducing insular heating close to the ground (Körner 2003). Studies have shown that exposure to harsh winds can explain major differences in plant communities (Hoare et al. 2000), especially on a macro-scale level (Mark et al. 2000). While all plants on exposed ridges generally experience severe mechanical wind stress, at a smaller-scale, near-by rocks and plants can provide shelter from these stresses (Körner 2003). An increase in wind toward the summit, which we did not measure directly but noticed while sampling ridges, might help explain the distribution of HD and LD vegetation. While most studies compare the effects of winds at very different topographical features (e.g., slope versus ridge, Billings 2000), our study suggests that there may also be notable variation in wind effects within these features.

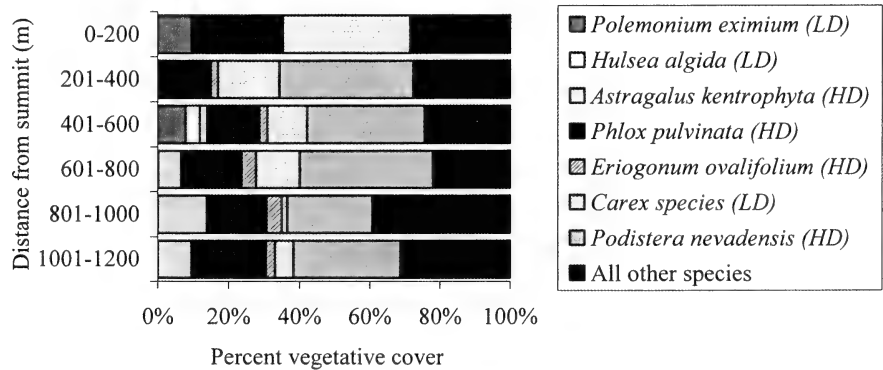


FIG. 2. Percent cover of High Diversity/Cover (HD) and Low Diversity/Cover (LD) species at increasing distances from the summit.

One might expect only the low-growing cushion plants to survive the harsh winds of the exposed summit. Counter to this intuition, however, our study showed that the most common species near the summit included large robust species (e.g., *Carex heteroneura*, *Polemonium eximium*, and *Hulsea algida*) and few low-growing species (e.g., *Calyptridium umbellatum*). If the wind is indeed fiercer at the summit, then how do these large plants that produce much of their above-ground biomass anew every year survive near the summit, and why aren't they found farther down?

Based on the physical architecture of the species found in HD and LD vegetation, we hypothesize that variation in the ability to colonize and persist may explain the divergence of these vegetation types. Conditions near the summit include fewer small rocks and possibly fiercer winds. These conditions may demand that the plant establish quickly and independently, using larger root systems and fueled by greater energy-collection from the above-ground portion of the plant. Farther from the summit, plants may take advantage of facilitative "nurse mats." Such mats formed by cushion species provide a warm protected shelter for smaller incoming species (Arroyo et al. 2003). In return, the new species would contribute nutrients and biomass to the micro-habitat and thus encourage increased colonization (Carlsson and Callaghan 1991). While it is generally assumed that abiotic physical attributes are by far the most important factors that govern alpine plant distributions (Crombie 1947; Körner 2003), these subtle biotic interactions might also be involved since the level of species diversity strongly helped define the vegetation patterns.

In summary, our data suggest that even at the relatively small scale limited to xeric alpine ridges, definable patterns of species composition and abundance do exist. The patterns we found were better defined by variation in species richness and cover (i.e., HD and LD vegetation) rather than solely groups of species defined by frequent co-occurrence. The ultimate governing factors defining these patterns may still be moisture availability and shelter from the wind, quantified in our study by aspect, rock size, and proximity to the summit. However, micro-habitat variation may be working at a much finer scale, which is less easily measured (e.g., sub-surface rock architecture). Our study has shown, that in order to fully understand the distributions and abundances of alpine plant communities, it is helpful to examine compositional patterns at a small scale.

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HERBIVORY AND THE ENDANGERED ROBUST SPINEFLOWER (*CHORIZANTHE ROBUSTA* VAR. *ROBUSTA*)

SANDRA BARON¹ AND SHANNON M. BROS

Department of Biology, San Jose State University, San Jose, CA 95192-0025

ABSTRACT

Insect herbivory has been shown to have substantial impacts on plant growth and reproduction in many systems. However, the effect of insect herbivores on rare and endangered plants has not been widely studied, even though natural limitations on growth and reproduction, in combination with anthropogenic changes in habitat quality and quantity, likely contribute to population decline. In the current study, an insect exclusion experiment was used to assess the effects of insect herbivory on a federally listed endangered annual plant: *Chorizanthe robusta* var. *robusta* (Polygonaceae). The primary insect herbivore was a microlepidopteran larva, an undescribed species of *Aroga* (Gelechiidae). Excluding *Aroga* larvae led to a 30% increase in seed output compared to water control. No change in plant survivorship or seed/flower ratios was found with insect exclusion. Control plants given supplemental water had increased seed production, but only in the absence of *Aroga* infestation, an indication that infested plants could not fully exploit additional resources. These results show that rare annuals are potential host plants for insect herbivores, and herbivory is an important factor to consider when evaluating endangered plant populations.

Key Words: insect exclusion, rare plants, sand dunes, *Aroga*, Gelechiidae.

Endangered plants characteristically have populations that are limited in size and extent, often due to habitat loss caused by human activities. In coastal areas of California, urban development and agriculture have reduced natural areas considerably. Under these conditions, any additional factor that reduces survivorship or reproduction of a rare species can contribute to the possibility of extinction. Numerous studies have shown that insect herbivores reduce survivorship, growth, and reproductive output of plants (Rausher and Feeny 1980; Louda 1982, 1984; Crawley 1983, 1989). In many cases plant fecundity is more dramatically limited by herbivory than is survivorship, and an increase in seed number is often found when herbivores are excluded, even when herbivory is at very low levels (Crawley 1983; Kinsman and Platt 1984; Brown et al. 1987; Root 1996; Wise and Sacchi 1996; Mauricio 1998; Parmesan 2000; Maron 2001). Leaf and flower damage from herbivory can also indirectly affect seed production by decreasing pollination rates (Mothershead and Marquis 2000). Although these effects of herbivory on plant performance are well documented, the question of how herbivores affect plant populations is still widely debated (Crawley 1983, 1989; Carson and Root 2000). Some studies have shown that a reduction in seed by herbivores is likely to lead to a reduction in plant abundance (Louda 1982; Louda and Potvin 1995; Wise and Sacchi 1996; Fagan and Bishop 2000; Maron 2001), but density-dependent mortality or a shortage of germination sites can negate

this effect (Crawley and Gillman 1989; Maron and Gardner 2000). However, research has shown that small populations of endangered plants can be restricted by low seed production (Pavlik et al. 1993; Bevill et al. 1999) so we can not discount herbivory when evaluating rare plants. Plants can be rare for a variety of reasons (see Rabinowitz 1981), but the end result is often small population size. Projections of population growth or decline are impossible to make without first identifying the factors which reduce plant survivorship and reproduction, and discerning the vulnerable life stages (Pavlik et al. 1993; Schemske et al. 1994).

Excluding herbivores from a subset of plants and comparing plant performance is the best way to assess the effects of herbivory in wild plant populations (Crawley 1989), and this was the method used for this study. Plant competition and availability of resources must also be considered, as these factors can work in concert with herbivory to affect plant growth and reproduction. For example, limited resources can increase the effect of herbivory on individual plants by restricting growth (Louda 1984; Louda et al. 1990), but some studies have shown that even when resources are plentiful, plants cannot overcome the effects of herbivory, especially annual plants (Pavlik et al. 1993; Wise and Sacchi 1996).

The current study seeks to determine if insect herbivory reduces survivorship, growth, and seed output of *Chorizanthe robusta* var. *robusta* C. Parry (Polygonaceae), a federally listed endangered plant. Mammal herbivores are often important in sand dune habitats (Palmisano and Fox 1997); however, no mammal herbivory was seen in preliminary

¹ Current address: 119 Rancho Road, Watsonville, CA 95076-9608. e-mail: logic@ispwest.com

studies on *C. robusta* at two sites over two years (personal observation), and Swank and Oechel (1991) noted that rabbits rarely grazed *Chorizanthe fimbriata* and *C. polygonides* in their study in chaparral. Consequently, only insects were excluded in this study.

Herbivore density can vary between small and large patches of host plants (Bach 1988). Because herbivore density patterns are an important factor in predictive models, the relationship between clearing size and herbivory was also investigated.

METHODS

Plant Species

Chorizanthe robusta var. *robusta* is an annual spineflower that inhabits sandy soil sites in Santa Cruz County, CA. Plants are low-growing and extremely variable in size, forming a single upright stem or having multiple branches. *Chorizanthe robusta* germinates in the winter and flowers from April through June or July. Each plant produces multiple small flowers and each flower can produce one seed. Seeds are dispersed in involucre with hooked awns that can attach to passing animals. *Chorizanthe* colonizes along trails and in clearings over the landscape. At the study site, some of these clearings are very large with thousands of plants and others are small with only a few individuals encircled by shrubs. This plant is federally listed as endangered and is known from seven populations, some less than 100 plants (USFWS 2000). The genus *Chorizanthe* is taxonomically challenging, with many closely related species, subspecies, and varieties in California (Ertter 1996). There are taxonomic uncertainties about *C. robusta* at the study site due to the proximity of a closely related species *Chorizanthe pungens* (Benth). *Chorizanthe pungens* is thought to grow primarily on the fore dunes and *Chorizanthe robusta* primarily on the rear dunes; however, no published studies have quantified the genetic structure of the species complex. The plants chosen for this study were on the rear dunes and morphologically similar to *Chorizanthe robusta* var. *robusta* at other sites.

Insect Herbivore

Although this study examined the effect of excluding all chewing insects, the primary insect herbivore on *C. robusta* were larvae of an undescribed moth species in the genus *Aroga* (Gelechiidae) (J. Powell personal communication). These larvae create silken shelters covered with sand and litter, attached to the base of *C. robusta* plants. They feed on leaves and are active from March through June. Pupation occurs in shelters on or near the soil surface. Adult specimens were collected in the field in early August.

Study Site

Sunset State Beach was selected as the location for this study because the largest known population of *C. robusta* (many thousands of plants) occurs over a wide area on the rear dunes. Sunset State Beach is located in central California just west of the town of Watsonville (36°52.89'N, 121°49.69'W). The study site was within a 300 square meter area on the top of a rear dune. These rear dunes are stable and dominated by coastal scrub species such as *Ericameria ericoides* (Less.) Jepson (Asteraceae). The habitat is a mosaic of various sized openings between shrubs with sand, moss, grasses, bracken fern, and forbs. *Chorizanthe robusta* grows in dense patches in these openings. Much of the study site is colonized by *Syntrichia princeps* (De Not.) Mitt [*Tortula princeps*], a low growing moss that forms mats in which *C. robusta* and other forbs grow.

The central coast of California has a moderate mediterranean climate. During the study period (October 2000–April 2001), the average monthly temperature of 12°C was normal for this period. An average monthly rainfall of 2.4 inches was 79% of normal for this period. The last measurable rainfall for the season was on or about April 18, 2001 (U.S. Dept. of Commerce 2002).

Experimental Design

An insect exclusion experiment with three treatments was performed to assess the effects of herbivory on plant survivorship, plant size, and seed output. In one set of plants insects were excluded by using an insecticide spray, Carbaryl (1-naphthol *N*-methylcarbamate), a ready-mixed aqueous solution of a wide-spectrum carbamate insecticide, brand name Sevin (Rhone-Poulenc). Carbaryl kills chewing insects for three to ten days, and has a half life of seven days in aerobic soil (PMEP 1993). Prior studies on this insecticide indicate that its effects on plant growth are minimal (Jones et al. 1986; Gibson et al. 1990). Because spraying of water may influence growth and seed production, two controls were included to assess the effect of insect exclusion with an insecticide independent of spraying. The first control included plants that were sprayed in the same manner as the insecticide but with water only. For the second control, the plants were not sprayed. Every seven to ten days from March 17 to May 14, 2001, until plants were in flower, insecticide and water spray treatments were applied in the morning when winds were calm and temperatures low.

A randomized block design was used to minimize effects from microhabitat variation. Fifty blocks, each with three plants of similar size growing near each other, were randomly selected. Each plant in the block was assigned a different treatment, and the order of assignment was randomized.

Four types of measurements were made. Plants were inspected weekly for the duration of the study

TABLE 1. RANDOMIZED COMPLETE BLOCK ANCOVA FOR TESTING THE EFFECT OF EXCLUDING INSECT HERBIVORES ON NUMBER OF SEEDS PER PLANT. Independent variable was Treatment with three levels, Insect exclusion (IE), Water spray control (W), and Non-spray control (N). Dependent variable was number of seeds per plant (ln transformed). Blocks were randomly selected groups of three plants. Covariate was final plant density.

| Source | SS | df | MS | F | P |
|---------------------|--------|----|-------|-------|-------|
| Treatment | 9.401 | 2 | 4.700 | 3.657 | 0.038 |
| IE vs. W | 7.305 | 1 | 7.305 | 5.683 | 0.023 |
| W vs. N | 0.004 | 1 | 0.004 | 0.003 | 0.956 |
| Block | 31.478 | 16 | 1.967 | 1.530 | 0.151 |
| Final Plant Density | 8.983 | 1 | 8.983 | 6.989 | 0.013 |
| Error | 39.848 | 31 | 1.285 | | |

to monitor survivorship and determine whether they had been infested with *Aroga*. Local plant density was measured at the beginning and end of the experiment by positioning each study plant in the center of a 10-cm square, and counting all plants within the square. In addition, the size of each clearing (with study plants) was measured. After seed set, plants were collected to measure plant size, number of seeds, and number of flowers. Because *Chorizanthe robusta* has small sparsely distributed leaves along with highly variable stems and branches, the sum of the length of all branches plus the length of the stem was used as a measure of plant size. For each plant, seed/flower ratios were also computed.

Randomized Complete Block Analysis of Covariance (Zar 1996) was used to assess the effect of excluding insect herbivores on plant size (total length of branches plus stem), number of seeds, and seed/flower ratios. For all analyses, the independent variable was Treatment with three levels, insect exclusion by application of insecticide, water spray control, and the non-spray control. Plant size and number of seeds were transformed for analysis as $\ln(x)$ because variances of the untransformed variables were not homogeneous among treatments. Blocks in the analyses were the randomly selected groups of plants. To insure that the treatments within a block really represented cases where herbivores were excluded or not, only those blocks in which *Aroga* occurred were considered for analyses. Blocks in which one or more plants died or in which grazing by rabbits occurred during the experiment were also excluded from analyses. For each dependent variable, two a priori comparisons were performed to compare treatments. To assess whether the application of insecticide affected plant size or number of seeds, the insect exclusion treatment was compared to the water spray control. Because final plant density was correlated with plant size ($r = -0.493$) and number of seeds ($r = 0.484$), final plant density was included in the analyses as a covariate. To determine if there was a difference in the effect of watering between infested and non-infested plants, all watered plants were analyzed using ANCOVA with Infested as the independent variable, and seed number and plant size as dependent

variables. Final plant density was included as a covariate.

To evaluate the effect of plant patch size on sources of herbivory, 145 plants in patches of varying sizes were examined throughout the study period. Patches were identified as groups of plants surrounded by shrubs. The area of each patch was measured in square meters (length \times width). Patches were classified by area into three groups: Small: 0–3.00 m², Medium: 3.01–7.00 m², and Large: 7.01–10.00 m². Evidence of rabbit grazing and infestation by *Aroga* was recorded for each patch. A 2×2 Test of Independence (Zar 1996) was used to determine if there was a relationship between the presence or absence of rabbit grazing and patch size. The same type of test was used to determine if the presence or absence of *Aroga* larvae was independent of patch size.

RESULTS

Plant mortality was extremely low during this study. Only two (out of 150) study plants died and both were due to gopher activity. However, rabbits (*Sylvilagus bachmani* Grinnell and Storer) removed mature seed heads late in the season from 11% of study plants, effectively eliminating their reproductive potential.

The RCB ANCOVA showed that seed number increased when insects were excluded (Table 1). The first a priori comparison showed that mean number of seeds per plant (ln transformed) was greater ($P < 0.023$) in the insect exclusion treatment as compared to the water spray control (Fig. 1). The second a priori comparison showed that mean number of seeds per plant did not differ ($P = 0.956$) between the water spray control and the non-spray control (Fig. 1). The block effect was not significant ($P = 0.151$) indicating that a block design was not necessary. However, final plant density was a significant covariate ($P = 0.013$). ANCOVA for seed/flower ratios showed no significant difference among treatments ($P = 0.211$).

The results for plant size were similar to the results for number of seeds (Table 2). The RCB ANCOVA showed that plant size increased when insects were excluded. The first a priori comparison

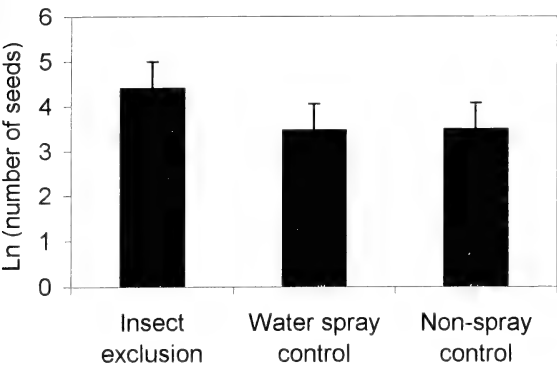


FIG. 1. Mean number of seeds per plant (ln transformed) for the three treatments, Insect exclusion, Water spray control, and Non-spray control, adjusted for final plant density. Error bars are 95% confidence limits.

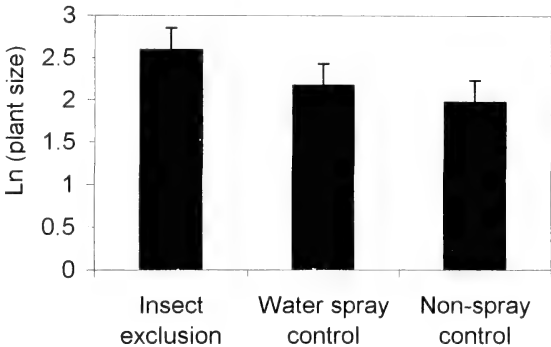


FIG. 2. Mean plant size per plant (cm) (ln transformed) for the three treatments, Insect exclusion, Water spray control, and Non-spray control, adjusted for final plant density. Error bars are 95% confidence limits.

showed that mean length of branches plus stem per plant (ln transformed) was greater ($P < 0.026$) in the insect exclusion treatment as compared to the water spray control (Fig. 2). The second a priori comparison showed that mean length of branches plus stem per plant did not differ ($P = 0.273$) between the water spray control and the non-spray control. The block effect was barely significant ($P = 0.050$) indicating that a block design was desirable for experiments in which plant size was the measured variable. As with the analysis for number of seeds, final plant density was a significant covariate ($P = 0.040$).

The effect of watering differed for infested vs. non-infested plants. Average seed number was significantly higher for non-infested plants ($P < 0.02$) and final density was an important covariate (Table 3, Fig. 3).

Both rabbit grazing and presence of *Aroga* larvae appeared to be related to plant patch size. The results of the 2×2 Test of Independence showed that plant patch size was related to the presence or absence of rabbits (Log-likelihood ratio = 23.508, df = 2, $P < 0.001$); rabbit grazing tended to occur more often in the smallest plots (Fig. 4). Patch size was also related to the presence or absence of *Aroga* larvae (Log-likelihood ratio = 9.415, df = 2, $P < 0.010$). During this study, 34% of plants not

sprayed with insecticide had signs of *Aroga* infestation and *Aroga* larvae tended to appear in larger patches of plants (Fig. 5).

DISCUSSION

The results of this study indicate that insect herbivores significantly reduced both size and lifetime seed production of these annual plants, factors that could have far reaching effects on a small population (Table 1). Since seed/flower ratios did not differ for insecticide treated plants, insects reduced seed production by reducing plant size (or resource allocation) rather than pollination rates. Plant size has often been found to be correlated with seed output (Rausher and Feeny 1980; Wolfe 1983; Brown et al. 1987; Stöcklin and Favre 1994). Potential growth effects from insecticide use must also be considered. In the absence of herbivory, insecticide treated plants were no larger on average (16.8 cm) than plants sprayed with only water (17.2 cm). Because other studies have shown that Carbaryl has a negative or minimal effect on plant growth (Jones et al. 1986; Gibson et al. 1990) it is unlikely that Carbaryl induced plant growth in this study.

Additional water increased seed output, but only in plants without *Aroga* infestation (Fig. 3). Other studies have also found that abundant or supplemental water did not produce an increase in seed

TABLE 2. RANDOMIZED COMPLETE BLOCK ANCOVA FOR TESTING THE EFFECT OF EXCLUDING INSECT HERBIVORES ON PLANT SIZE. Independent variable was Treatment with three levels, Insect exclusion (IE), Water spray control (W) and Non-spray control (N). Dependent variable was total branch length plus stem per plant (ln transformed). Blocks were randomly selected groups of three plants. Covariate was final plant density.

| Source | SS | df | MS | F | P |
|---------------------|-------|----|-------|-------|-------|
| Treatment | 2.237 | 2 | 1.619 | 6.091 | 0.006 |
| IE vs. W | 1.449 | 1 | 1.449 | 5.454 | 0.026 |
| W vs. N | 0.331 | 1 | 0.331 | 1.245 | 0.273 |
| Block | 8.424 | 16 | 0.527 | 1.981 | 0.050 |
| Final Plant Density | 1.223 | 1 | 1.223 | 4.602 | 0.040 |
| Error | 8.239 | 31 | 0.266 | | |

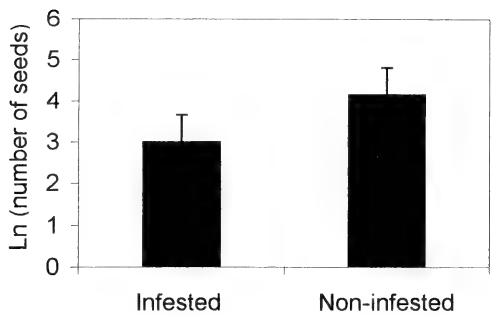


FIG. 3. Mean number of seeds per plant (ln transformed) for infested vs. non-infested water sprayed plants, adjusted for final plant density. Error bars are 95% confidence limits.

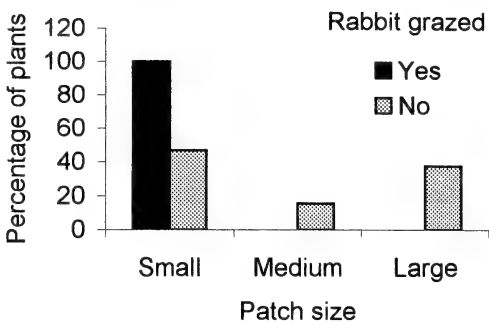


FIG. 4. Plant patch size (small = 0–3.00 m², medium = 3.01–7.00 m², large = 7.01–10.00 m²) vs. presence or absence of rabbit grazing.

output in plants subject to herbivory (Swank and Oechel 1991; Pavlik et al. 1993; Wise and Sacchi 1996). Because *Aroga* larvae remove leaves, they compromise the plant’s ability to garner resources (Louda 1984; Louda et al. 1990). This potential interaction between herbivory and resource uptake and allocation is an important factor to consider in rare plant management. If models are used to predict plant population growth, it may be necessary to include potential differences in resource utilization by the proportion of the population subject to insect herbivory.

Decreased seed production is a potential threat to the long term viability of this plant population only if it is seed limited (Louda 1982; Crawley 1983, 1989). A reduced seed supply may not affect a population with a shortage of “safe sites” for germination (Crawley and Gillman 1989). However, “safe site” availability can be difficult to determine because it can vary over years and over the landscape (Maron and Gardner 2000). In sand dune habitats it is likely that the availability of germination sites fluctuate yearly due to shrub growth and small scale disturbances. Research has shown that annual plants in sand dune environments often show evidence of seed limitation (Turnbull et al. 2000). Seed reduction can also have a greater impact on a plant species, such as *C. robusta*, that has metapopulation dynamics (Bevill et al. 1999), defined as sub-populations connected by dispersal (Eriksson 1996). Ecological factors such as these, combined with a loss of habitat due to human activities, may intensify the effects of herbivory and

cause proportionally greater threats to rare and endangered plant populations.

There was some evidence that herbivores were selecting plants based on an environmental condition: clearing size. Larvae were more often found in the largest clearings, and rabbit grazing was more prevalent in small clearings and at the edges where shrubs were dense (Figs. 4 and 5). Herbivore density patterns will be important to include in predictive models, but they may also have evolutionary consequences. According to John Thompson (personal communication), selection based on an environmental variable can increase the potential for genetic polymorphisms. In addition, the discovery of a possibly specialist herbivore presents future research opportunities that may help shed light on *Chorizanthe* taxonomy. Evolutionary relationships between species can evolve over small time scales, even decades, and changes in the distribution of metapopulations are one of the “normal processes of evolution” (Thompson 1998). More research is needed to determine if this moth species is a specialist on *Chorizanthe*. Although it is unusual for an annual plant to have a specialist herbivore (Crawley 1983), most small moths are specialists and they can survive in small habitat patches (Powell 1999). In a study of the range size of host plants for a variety of insect herbivores in England, Hopkins et al. (2002) found that a number of “micro moths” were associated with rare plants. Microlepidoptera such as these are not well studied and 50% to 90% of species with small adults col-

TABLE 3. ANCOVA FOR TESTING THE EFFECT OF WATER ON SEED NUMBER. Independent variable was Infestation with two levels, Yes (Y) and No (N). Dependent variable was number of seeds per plant (ln transformed). Covariate was final plant density.

| Source | SS | df | MS | F | P |
|---------------------|--------|----|--------|--------|-------|
| Y vs. N | 8.857 | 1 | 8.857 | 6.094 | 0.020 |
| Final Plant Density | 29.770 | 1 | 29.770 | 20.483 | 0.000 |
| Error | 39.241 | 27 | 1.453 | | |

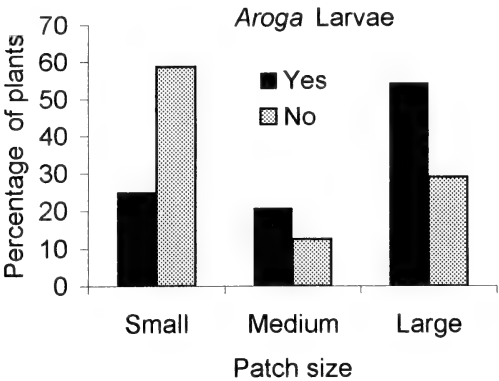


FIG. 5. Plant patch size (small = 0–3.00 m², medium = 3.01–7.00 m², large = 7.01–10.00 m²) vs. presence or absence of *Aroga* larvae.

lected in California, remain undescribed (Powell 1999). This little known group is likely closely associated with our native flora. Rare plants are potential host plants for insects that are often cryptic and easily overlooked. These insects may be endangered themselves, illustrating how the loss of an annual plant species can decrease biodiversity at multiple scales. Understanding these important relationships will help us to better understand the ecology of rare plants and help shed light on causes of yearly fluctuation in wild plant populations.

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HABITAT CHARACTERISTICS AND DISTRIBUTION OF *ERODIUM MACROPHYLLUM* (GERANIACEAE)

IAN G. GILLESPIE¹

Department of Botany and Plant Sciences, University of California,
Riverside, CA 92521

ABSTRACT

Ecological data are lacking for many species covered in multi-species habitat conservation plans and other regional conservation plans. *Erodium macrophyllum* (Geraniaceae) is a rare native annual forb found throughout California, southern Oregon, and northern Baja California (Mexico) for which very little ecology is known. I report on the habitat characteristics and current and historical distribution of *E. macrophyllum* by collecting data on populations in Riverside and San Louis Obispo Counties and by conducting an herbaria search and electronic-mail survey. *Erodium macrophyllum* population sizes range from a few individuals to over 1000 and are restricted to heavy clay soils. Most populations are found on the eastern side of the coast ranges in California. The clay soils on which it is found typically have low cover of native and exotic species but often have other rare species. They are also generally low in nitrogen and phosphorus, but there is considerable variation. Based on herbaria records and the e-mail survey, *E. macrophyllum* was probably once more common and may have occurred on other soil types.

Key Words: California grasslands, clay soil, edaphic factors, habitat conservation plan, rare plants, *Erodium macrophyllum*.

The collection of ecological data for rare plants is crucial in developing effective conservation plans (Schemske et al. 1994). Very little research has been done on the ecology or biology of the rare forb, *Erodium macrophyllum* Hook and Arn (Geraniaceae, large-leaved filaree). The California Native Plant Society (2001) lists *E. macrophyllum* as a category “2,” meaning that it is rare in California but more common elsewhere. The only information on the biology of *E. macrophyllum* is scattered in various regional floras and usually only consists of notes regarding its growth habit, habitat, and flower color. However, some research has been done by a group in Spain working on the systematics of Geraniaceae, and they have placed *E. macrophyllum* into a new monotypic genus and proposed *California macrophyllum* as a new name (Aldasoro et al. 2002). For the purposes of this paper I will follow the nomenclature of Hickman (1993).

The soil and habitat preferences of *E. macrophyllum* are poorly understood. Recent observations suggest that *E. macrophyllum* currently occurs exclusively in clay soil (Boyd personal communication; Gillespie personal observation; Hale personal communication). However, some historical observations, while anecdotal, suggest that *E. macrophyllum* was once common in a broader range of soil textures. For example, Abrams (1904) wrote, “[*E. macrophyllum* is] common in grasslands” and Gray (1876) wrote, “Common in valleys and on the lower hills west of the Sierra Nevada, from San

Diego northward to the Sacramento Valley. Next to *E. cicutarium* this is the most abundant species.” Given the lack of specificity of such historical accounts, it is possible that *E. macrophyllum* used to occur on a variety of non-clay soil types.

Understanding the basic ecology of rare plants can aid in conservation plans (Simberloff 1988). For example, knowing the habitat requirements of species is paramount when creating reserves for specific target species. *Erodium macrophyllum* is one of more than 160 species included in the multi-species habitat conservation plan for Riverside County, CA, and one of the limits in designating habitat for these species is the little information available (Dudek and Associates 2003).

In this paper I describe the current habitat characteristics of *E. macrophyllum* and its historical distribution and abundance. I also report on the results of a field and electronic-mail survey to better quantify its present distribution. The results of this study are discussed in the contexts of conservation and natural history.

MATERIALS AND METHODS

Study Species

Erodium macrophyllum is a rare annual plant apparently restricted to clay soil outcrops. Like many grassland annuals in California, *E. macrophyllum* germinates in fall or winter at the onset of the winter rains and usually flowers between March and May (Munz 1974). *Erodium macrophyllum* forms a basal rosette until it bolts in the spring when it sends up determinate and/or indeterminate umbellate inflorescences. The size of the basal rosette can

¹ Current address: 181 Westminster Road, Putney, VT 05346. e-mail: ian@igsoftware.com

vary from a few centimeters in diameter to at least 30 cm (Hickman 1993).

Erodium macrophyllum is self-compatible and will self-pollinate in the field. This has been confirmed by field and greenhouse observations. The flowers of *E. macrophyllum* are open for only one day and the petals usually only remain on the flower until mid-day. The anthers dehisce in the morning and after the petals drop, the anthers enclose the stigma and effectively pollinate it (personal observation). When the fruits of *E. macrophyllum* mature, the carpel bodies detach from the fruit base and peel away from the style column. When a carpel body finally releases from the style column it propels itself up to 1.25 m from the parent plant, although further dispersal may occur with wind (personal observation).

Habitat Characteristics

Soils from five different *E. macrophyllum* populations were sampled and analyzed for nutrients (N, P, Ca, Mg). Two populations (Davis Road and Bitterwater Road) were located in eastern San Luis Obispo County (35.50206°N × 120.07846°W; 35.71380°N × 120.26716°W, respectively). The other three populations were from western Riverside County: Bachelor Mountain (33.6006°N, 117.0528°W), Oak Mountain (33.5156°N, 116.9767°W) and De Palma Road (33.7416°N, 117.4387°W). For comparison purposes, soils were also collected from the Santa Rosa Plateau Ecological Reserve (Riverside Co., CA, USA) and from Crown Valley in the Lake Skinner/Shipley Multi-Species Reserve (Riverside Co., CA, USA). The additional locations were chosen because they are sites where I have re-introduced *E. macrophyllum*. Each soil core was 15 cm deep by 2 cm in diameter and at least 1 m from all other sample cores. The cores from the Bachelor Mountain and De Palma Road populations were collected April 2000, Bitterwater Road and Davis Road were collected in April of 2002 and Oak Mountain in January 2003. The samples were analyzed for total percent Kjeldahl N, extractable Olsen-P, and extractable Ca⁺⁺ and Mg⁺⁺ at the Soil Analytical Laboratory of the Division of Agriculture and Natural Resources, University of California, Davis, California. For soil nutrient data student t-tests were used to determine whether the measured variables differed significantly between site locations. Soils were identified using soil survey maps from Riverside County (Knecht 1971) and San Luis Obispo County (Lindsey 1983).

At each population site I recorded percent cover of three life form groups (exotic grass and native and exotic forbs) from five randomly placed 1.0 × 0.5-m quadrats. Percent cover was estimated to the nearest 1% using a gridded frame. For the Davis Road and Bitterwater Road populations, the estimates were made in April 2002 and for the De Pal-

ma Road, Oak Mountain and Bachelor Mountain populations the estimates were made in March 2003. For the percent cover data, a multiple analysis of variance (MANOVA) was used to determine if the plant communities at each population differed significantly from one another based on the dependent variables measured (species groups: native forbs (excluding *E. macrophyllum*), native grass, *E. macrophyllum*, exotic forbs and exotic grass). Because the two sites in San Luis Obispo County were sampled in a different year than the Riverside County sites, separate MANOVAs were conducted for the populations in San Luis Obispo County and Riverside County.

Survey of Occurrence

The current distribution of *E. macrophyllum* was determined by examining herbaria records from seven different herbaria (Rancho Santa Ana Botanic Garden, University of California Riverside, Jepson Herbarium, University of Arizona, Utah State University, California Academy of Sciences, San Jose State University), searching the California Natural Diversity Database (CNDDDB) and by conducting an electronic-mail survey to 255 professional botanists throughout the western United States. The following questions were asked in the survey: 1) How many populations of *E. macrophyllum* do you know of in your area? 2) Approximately how many individuals are/were in each population? 3) If you recall, on what type of soil were the populations found? 4) If you recall, what associated species were growing with *E. macrophyllum*? 5) Is/are the population(s) that you know of accessible, if so, would you be willing to take me to it/them? 6) Do you have any additional concerns/comments regarding *E. macrophyllum*?

RESULTS

Habitat Characteristics

The soil from the Santa Rosa Plateau site was classified as a clay loam in the Monserate series and Crown Valley as a sandy loam from the Friant series (Knecht 1971). Bachelor Mountain, De Palma Road and Oak Mountain soils were classified as clay from the Auld series (Knecht 1971). Soils from the Davis Road and Bitterwater Road populations were classified as a clay in the Diablo series (Lindsey 1983). The clay soils tended to be low in total N, low in extractable P, but the Ca:Mg ratios were high (Fig. 1). Although there were differences in Ca:Mg between sites, none of the clay soil sites had Ca:Mg less than 1.0 as can be found on serpentine soils (Harrison 1999). Crown Valley had the highest phosphorus and this site may have been historically cultivated; it also was the only sandy loam soil analyzed.

For the five sites I sampled, mean percent cover of bare ground varied from 16–89. Within San Lou-

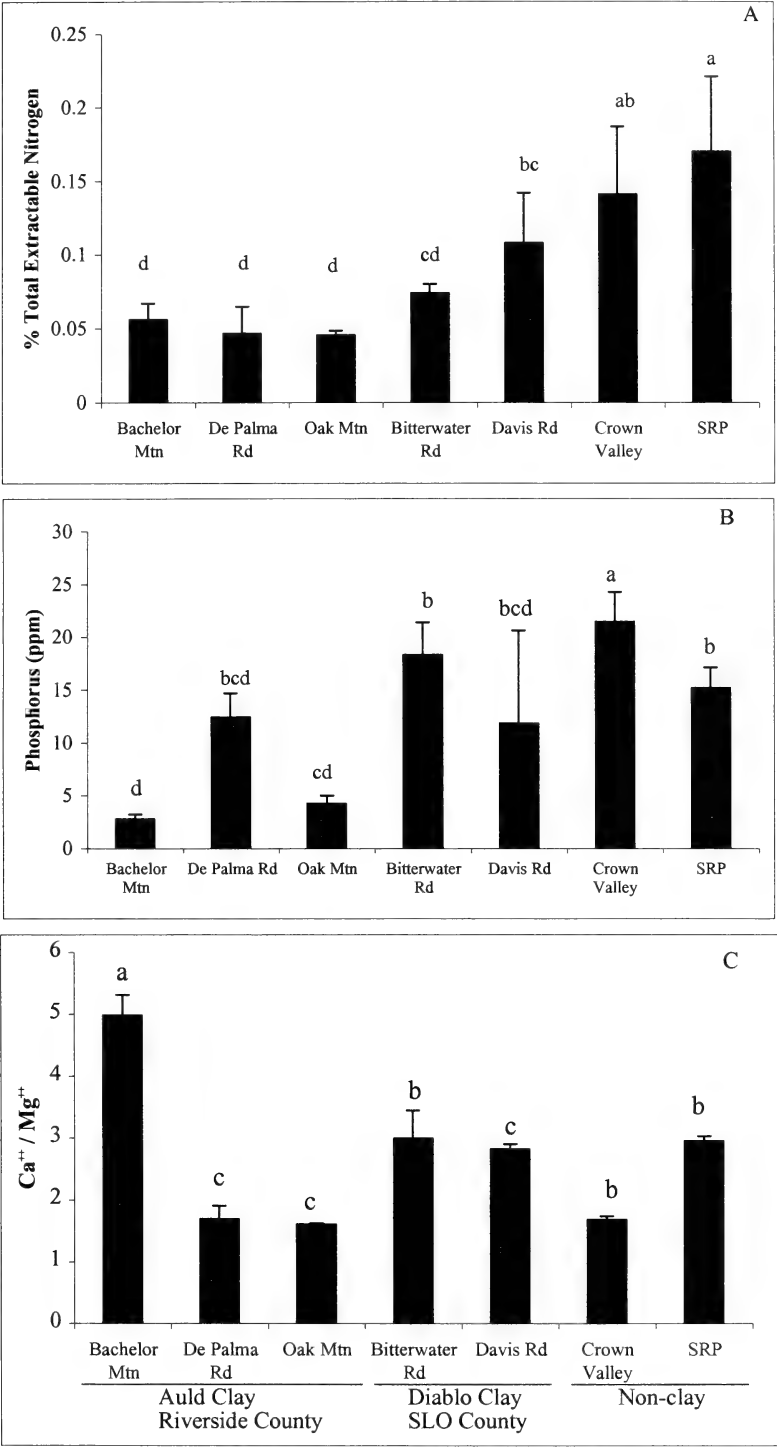


FIG. 1. Percent total extractable nitrogen (NO_3 plus NH_4) (A), extractable Olsen-Phosphorus (B) and Ca:Mg ratio (C) for different sites with and without *Erodium macrophyllum*. Crown Valley and SRP (Santa Rosa Plateau) do not have naturally occurring populations of *E. macrophyllum*. Bars are means \pm SE ($N = 5$). Different letters indicate a significant difference between populations ($P < 0.05$).

TABLE 1. CHARACTERISTICS OF FIVE POPULATIONS OF *ERODIUM MACROPHYLLUM*. Different letters indicate a significant difference between locations within counties based on the percent cover data shown (MANOVA, $P < 0.05$).

| Location | County | Popula- tion size (# indi- viduals) | Percent cover \pm SE | | | | <i>Erodium</i> <i>macro-</i> <i>phyllum</i> |
|------------------------------|------------------|--|------------------------|-----------------|-----------------|-----------------|---|
| | | | Native Forbs | Exotic Forbs | Native Grass | Exotic Grass | |
| Bachelor Mtn. ^a | Riverside | 80–100 | 4.8 \pm 1.4 | 10.2 \pm 2.3 | None | 6.4 \pm 1.8 | 2.6 \pm 0.7 |
| De Palma Rd. ^b | Riverside | ~700 | 17.2 \pm 3.6 | 22.4 \pm 7.4 | None | 21.0 \pm 11.5 | 10.8 \pm 2.8 |
| Oak Mountain ^c | Riverside | ~10 | 5.2 \pm 1.5 | 0.8 \pm 0.2 | 2.6 \pm 1.9 | 0.6 \pm 0.3 | 1.6 \pm 0.4 |
| Bitterwater Rd. ^a | San Louis Obispo | ~1000 | 9.6 \pm 3.1 | 9.4 \pm 2.4 | None | 39.4 \pm 4.6 | 5.6 \pm 4.2 |
| Davis Rd. ^b | San Louis Obispo | ~200 | 32.2 \pm 17.3 | 29.6 \pm 7.1 | None | 19.0 \pm 5.3 | 3.2 \pm 1.2 |

is Obispo County, percent cover classes at the Bitterwater Road site were different from the Davis Road site (MANOVA $F_{4,10} = 7.326$, $P = 0.0254$). An ANOVA showed that all species groups differed between the two sites except for their percent cover of *E. macrophyllum* (Table 1). The Riverside County sites differed significantly from each other also (MANOVA $F = 3.335$, $P = 0.0162$). The De Palma Road site had greater percent cover of native forbs and *E. macrophyllum* than the other Riverside County sites. It also had a greater cover of exotic forbs, but only when compared to the Oak Mountain site. The Oak Mountain population had the lowest cover of all species groups, but it was also the only population to have the native grass, *Nassella cernua*.

Several other rare plants can also be found growing in the clay soil habitats where *E. macrophyllum* is found. Rare plants recorded growing in these habitats include: *Allium munzii*, *Harpoganella palmeri*, *Convolvulus simulans*, and *Calochortus clavatus* var. *clavatus*, although not all sites contain them. Other more common plants that can co-occur with *E. macrophyllum* are found in Appendix 1.

Survey of Occurrence

Eighty-three herbaria records were obtained from the seven different herbaria. Seventy-three records were found in the CNDDb, most of which matched herbaria records. From the email survey there were a total of 31 responses: 18 reported that it did not occur in a specific geographic area (question 2 from the survey) and 13 reported that they knew of a population. However, several of the responses that indicated the presence of a population matched a record of either an herbarium sheet or a record from the CNDDb. After removing obvious duplicate records from all of the sources in which the description, location and date matched, I determined that a total of 105 unique populations of *E. macrophyllum* have been documented, most of which occur on the eastern side of the California coast ranges (Fig. 2). The first population was documented in 1862 by W. Brewer as part of a California State survey. The most recent populations were noted in 2002 through the email survey. Of these 105 records, 62% mentioned it was found on clay, while

the other 28% didn't mention a soil type. Clay soils were first mentioned in the 1930s.

Only a few of the historical sites have been revisited. For example, there is one occurrence of *E. macrophyllum* for Butte County, CA, but it has not been found there again despite extensive surveying. Furthermore, it is possible that it never occurred in Butte County, and the possible misinformation for Butte County may be based on a mislabeled specimen (Lawrence Janeway personal communication). Similarly, *E. macrophyllum* was collected from Santa Cruz Island, California, in 1888 (K. Brandagee, no collection number), yet it has not been re-discovered (Steve Junak personal communication).

Populations of *E. macrophyllum* are also being discovered and extirpated in recent years. For example, *E. macrophyllum* was collected near Murrieta, Riverside County, in 1998 (J. Easton, no collection number), but repeated visits to the site have revealed that the population has been lost to a housing development.

Erodium macrophyllum was previously thought to be found in California, northern Mexico and southern Utah (Hickman 1993). However, *E. macrophyllum* was never collected in Utah and the incorrect information in The Jepson Manual (Hickman 1993) is apparently based on a mislabeled specimen (James Morefield personal communication). (This also explains why the Utah State Herbarium had no records of *E. macrophyllum*.)

Erodium macrophyllum should now be considered endemic to the California floristic province with occurrences on either side of California's north and south borders. I found one collection from Oregon (collected in 1887) and three collections from Baja California (Mexico) dating 1931, 1949, and 1958.

The size of *E. macrophyllum* populations tend to be small ranging from 6–1000 individuals. Of the known occurrences where population size was documented, three populations were estimated to have 100–1000 individuals, two populations had less than 100, five had 20 or less, two had six and one had a "handful of individuals."

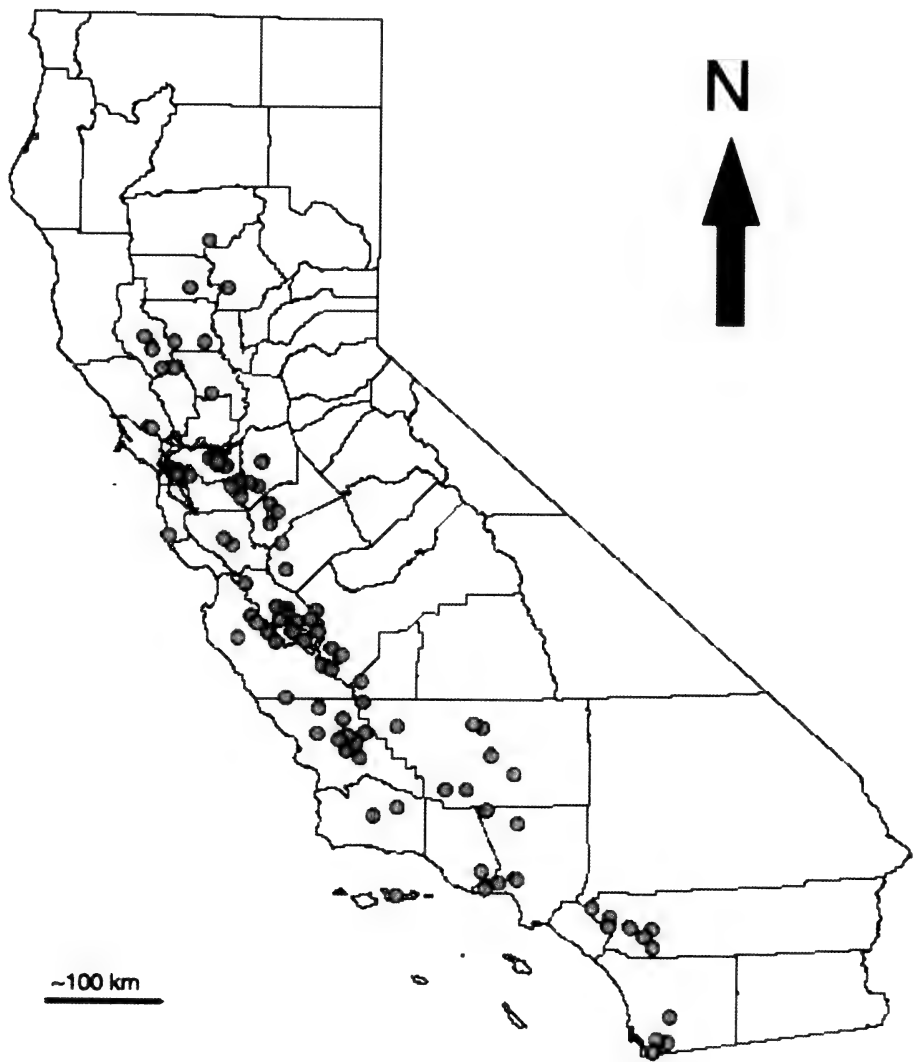


FIG. 2. Known distribution of *Erodium macrophyllum* populations in California based on current and historical occurrences. Circles represent approximate locations of populations. County lines are delineated on the map.

DISCUSSION

Erodium macrophyllum is apparently restricted to heavy clay soils. One hypothesis on edaphic endemism is that endemics are less competitive on other soil types (Wright and Mooney 1965), while tolerating the unfavorable conditions of low productivity environments (Grime 1973; Goldberg and Novoplansky 1997). The clay soils on which *E. macrophyllum* is found are low in nutrients, and the clay texture may restrict water infiltration and root penetration (Knecht 1971; Lindsey 1983).

Percent cover of exotic grasses and forbs is low and bare ground is high on clay soils compared to other grassland soils, which often have no bare ground exposed (Dyer and Rice 1997; DiTomaso et al. 1999); although percent cover of groups can vary between clay soil sites even if they are relatively close to each other (within the same county).

While the exact mechanism that explains restriction of *E. macrophyllum* to heavy clay soils is not known, evidence suggests that there is no physiological barrier, and that they can actually grow and reproduce on other soil types (Gillespie 2001). In fact, *E. macrophyllum* produced more biomass when growing on non-clay soils than clay soils (Gillespie unpublished data). It is possible that the high cover and densities of exotic plants on non-clay soils results in an environment where *E. macrophyllum* is out-competed, and it is effectively restricted to clay soils where there is less competition.

The clay soils on which I sampled *E. macrophyllum* were low in N and P. Soils with unusual chemical or physical properties often support a higher diversity of native species and may resist invasion, as in serpentine soils (Huenneke et al.

1990; Harrison 1999). My results and observations suggest that grasslands on clay soils are not as invaded by exotic species as other grasslands in California. This is similar to Stromberg and Griffin's (1996) results where the invasive grass *Elymus caput-medusae* did not invade clay soils unless they were disturbed and the native bunch grass *Nassella pulchra* was most abundant on clay soils. Interestingly the exact mechanism by which clay soils can resist invasion is now known. The low percent cover of exotic species and the high species richness of rare taxa that can occur on clay soils make them important areas of conservation. Many heavy clay soil sites are found in relatively flat grasslands—the same places that are being developed rapidly, but should be considered for preservation.

Erodium macrophyllum is a rare plant today, although historical evidence suggests that it may have been more common. While there is much information missing from these original observations, they suggest that the distribution and perhaps abundance of *E. macrophyllum* has decreased in the last 100–120 years. For example, Olson (from the e-mail survey) wrote, “saw it once in disked field, may no longer be extant. Very rare in east bay [of San Francisco Bay Area].” While historical observations are valuable, their lack of detail can make them problematic for quantification. For example, the first documented occurrence of *E. macrophyllum* on clay was in 1934 (L. Short). It is possible that earlier collections were from clay soil, but the botanists did not mention it. Alternatively, perhaps *E. macrophyllum* was found on common soil types that were not clay, and the collector therefore did not think it was worth noting the soil type. Despite the uncertainties in the absence of specific detail from collection sites, it is fairly certain that *E. macrophyllum* is rare and usually found on clay soils.

Although some places where *E. macrophyllum* is found are not experiencing rapid development now, *E. macrophyllum* faces other threats such as off-highway vehicle activity and grazing. The De Palma Road population now has an off-highway vehicle course going directly through it, and during a visit to the Bitterwater Road population I observed cows happily ingesting the tender leaves of *E. macrophyllum* plants.

ACKNOWLEDGMENTS

Andrew Sanders was invaluable for requesting loan material from different herbaria. Special thanks to David Tibor for helping with the electronic-mail survey. Minh Dang and Hally Andersen helped with field work. Also, thanks to all of the botanists that helped with locating populations. Edith Allen, Jodie Holt and two anonymous reviewers provided helpful feedback on previous versions of this manuscript. Funding was provided by Southern California Botanists and California Native Plant Society.

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APPENDIX 1

Common species found growing with *Erodium macrophyllum*. Nomenclature from Hickman (1993).

NATIVE FORBS

- Achyrachaena mollis*
- Ancistrocarphus filagineus*
- Amsinckia mensiezii*
- Calochortus splendens*
- Lasthenia californica*
- Layia platyglossa*
- Lupinus succulentus*
- Plantago erecta*
- Salvia columbarae*
- Sisyrinchium bellum*

NATIVE GRASSES

- Nassella pulchra*
- Nassella cernua*

EXOTIC FORBS

- Erodium botrys*
- Erodium cicutarium*
- Centaurea melitensis*
- Hirschfeldia incana*
- Medicago polymorpha*

EXOTIC GRASSES

- Avena barbata*
- Avena fatua*
- Bromus hordeaceus*
- Hordeum* sp.

TAXONOMIC CHANGES IN *LESSINGIA* (COMPOSITAE: ASTEREAE)

STACI MARKOS

Jepson Herbarium, 1001 Valley Life Sciences Building #2465, University of California, Berkeley, CA 94720-2465
smarkos@socrates.berkeley.edu

ABSTRACT

Phylogenetic studies of *Lessingia* Cham. show that different corolla coloration (pink/white vs. yellow) diagnoses the two major clades of *Lessingia sensu stricto*. There are no taxonomic changes in the “pink/white group” but two taxa within the “yellow group,” recognized by Lane (1993) as *L. glandulifera* A. Gray and *L. lemmonii* A. Gray, are not monophyletic and have therefore been realigned to reflect natural lineages. The circumscription of *L. lemmonii sensu* Lane (1993) has been expanded and now includes the type specimen of *L. glandulifera*, a name that has priority over *L. lemmonii*. Plants included in a narrowed circumscription of *L. glandulifera sensu* Lane (1993) will now be recognized as *L. pectinata* Greene. *Lessingia glandulifera* A. Gray var. *peirsonii* (J. T. Howell) Markos and *L. pectinata* Greene var. *tenuipes* (J. T. Howell) Markos are new combinations.

Key Words: phylogeny, Asteraceae, Astereae, *Lessingia glandulifera*, *Lessingia lemmonii*.

The foundation for the taxonomic changes discussed here is a phylogenetic study of *Lessingia* based on morphological and molecular data (Markos and Baldwin 2001). Two genera, included in *Lessingia* by Lane (1993), *Corethrogyne* DC. (*L. filaginifolia*) and *Benitoa* D. D. Keck (*L. occidentalis*) will each be recognized as monospecific genera in the *Flora of North America North of Mexico*. Within *Lessingia (sensu stricto)*, corolla coloration (pink/white vs. yellow) diagnoses two major clades. There are no taxonomic changes in the “pink/white group” comprised of *L. arachnoidea* Greene, *L. hololeuca* Greene, *L. leptoclada* A. Gray, *L. micradenia* Greene, *L. nana* A. Gray, *L. nemaclada* Greene, *L. ramulosa* A. Gray, and *L. virgata* A. Gray. Within the “yellow group,” the circumscription of *L. germanorum* Cham., *L. tenuis* A. Gray (Cov.) will remain the same but two taxa, recognized by Lane (1993) as *L. glandulifera* A. Gray and *L. lemmonii* A. Gray (each with three varieties), are not monophyletic and have therefore been realigned to reflect natural lineages.

I expanded the circumscription of *L. lemmonii sensu* Lane (1993) to include plants that have yellow corollas, lack brown-purple bands in their corolla tubes, and have lanceolate style-branch appendages (0.3–1.3 mm long). The expanded circumscription includes the nomenclatural type of *L. glandulifera* (S. B. and W. F. Parish 577, August 1880, “Dry mesa, San Bernardino Valley,” San Bernardino County, California, deposited in the Gray Herbarium). Because *L. glandulifera* A. Gray, 1882, pre-dates *L. lemmonii* A. Gray, 1886, plants formerly bearing the name *L. lemmonii* must now bear the name *L. glandulifera* (Table 1).

I recognize three varieties of *L. glandulifera*: (1) *L. glandulifera* var. *glandulifera*, includes plants formerly recognized as *L. lemmonii* var. *lemmonii*,

L. lemmonii A. Gray var. *ramulosissima* (Nelson) Ferris, and some plants that were included in *L. glandulifera* var. *glandulifera* by Lane (1993); (2) *L. glandulifera* var. *peirsonii* with the same circumscription as *L. lemmonii* A. Gray var. *peirsonii* (J. T. Howell) Ferris; and (3) *L. glandulifera* A. Gray var. *tomentosa* (Greene) Ferris.

Lessingia glandulifera* A. Gray var. *peirsonii (J. T. Howell) Markos, comb. nov. Basionym: *Lessingia germanorum* Cham. var. *peirsonii* J. T. Howell, University of California Publications in Botany 16:26. 1929. Type: California, Los Angeles Co., Kings Canyon, Liebre Mountains, 9 May 1923, F. W. Peirson 3550 (CAS).

Lessingia pectinata Greene is the earliest available name for plants that have yellow corollas, brown-purple bands in their corolla tubes, and truncate-penicillate style-branch appendages. I recognize two varieties of *L. pectinata*: (1) *L. pectinata* Greene var. *pectinata* with the same circumscription as *L. glandulifera* A. Gray var. *pectinata* (Greene) Jepson; and (2) *L. pectinata* var. *tenuipes* comb. nov. includes some plants included in *L. glandulifera* var. *glandulifera* by Lane (1993).

Lessingia pectinata* Greene var. *tenuipes (J. T. Howell) Markos, comb. nov. Basionym: *Lessingia germanorum* Cham. var. *tenuipes* J. T. Howell, University of California Publications in Botany 16:20. 1929. Type: California, San Luis Obispo Co., 4 mi s of Templeton, 17 Aug 1927, J. T. Howell 3005 (CAS).

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I thank Dave Silverman for collecting specimens in Southern California, Bruce G. Baldwin, John L. Strother, Jeff Greenhouse, David J. Keil, and one anonymous re-

TABLE 1. SUMMARY OF TAXONOMIC CHANGES IN LESSINGIA (SENSU STRICTO).

| Lane (1993) | Markos (this study) |
|---|---|
| Yellow corollas without a brow-purple band in corolla tubes, style-branch appendages lanceolate | |
| <i>L. lemmonii</i> A. Gray var. <i>lemmonii</i> | <i>L. glandulifera</i> A. Gray var. <i>glandulifera</i> |
| <i>L. lemmonii</i> A. Gray var. <i>peirsonii</i> (J. T. Howell) | <i>L. glandulifera</i> A. Gray var. <i>peirsonii</i> (J. T. Howell) |
| Ferris | Markos |
| <i>L. lemmonii</i> A. Gray var. <i>ramulosissima</i> (Nelson) | <i>L. glandulifera</i> A. Gray var. <i>glandulifera</i> |
| Ferris | |
| <i>L. glandulifera</i> A. Gray var. <i>tomentosa</i> (Greene) | <i>L. glandulifera</i> A. Gray var. <i>tomentosa</i> (Greene) |
| Ferris | Ferris |
| <i>L. glandulifera</i> A. Gray var. <i>glandulifera</i> | <i>L. glandulifera</i> A. Gray var. <i>glandulifera</i> |
| Yellow corollas with a brow-purple band in corolla tubes style-branch appendages truncate-penicillate | |
| <i>L. glandulifera</i> A. Gray var. <i>glandulifera</i> | <i>L. pectinata</i> Greene var. <i>tenuipes</i> (J. T. Howell) |
| | Markos |
| <i>L. glandulifera</i> A. Gray var. <i>pectinata</i> (Greene) | <i>L. pectinata</i> Greene var. <i>pectinata</i> |
| Jepson | |

viewer for helpful comments on this manuscript. Specimens and type material were loaned from or observed in CAS, GH, JEPS, ND, UC, and US.

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A NEW COMBINATION IN *BOECHERA* (BRASSICACEAE)
FOR THE ROCKY MOUNTAIN REGION

NEIL SNOW

Department of Biological Sciences, University of Northern Colorado,
Greeley, CO 80639
neil.snow@unco.edu

ABSTRACT

The new combination *Boechea holboellii* (Hornem.) Löve & Löve var. *pendulocarpa* (A. Nelson) N. Snow is made to accommodate this taxon at the rank of variety in that genus for the Southern Rocky Mountain Flora project.

Key Words: nomenclature, Rocky Mountains, *Arabis*, *Boechea*.

During the recent preparation of a checklist of vascular plants for the Southern Rocky Mountains Flora Project (Snow and Brasher 2004) it became evident that a combination in the genus *Boechea* Löve & Löve (Brassicaceae) was unavailable at the varietal level for a taxon formerly recognized from that region as *Arabis holboellii* Hornem. var. *pendulocarpa* (A. Nelson) Rollins (Harrington 1954; Rollins 1993; Kartez and Meacham 1999; Welsh et al. 2003). The purpose of this brief article is to make the appropriate combination in the genus *Boechea*. The new combination is necessary given the mounting evidence that *Arabis sensu lato* is highly polyphyletic and that most North American taxa assigned to *Arabis* belong in *Boechea* (Weber 1982; Al-Shehbaz 2003 and references therein).

***Boechea holboellii* (Hornem.) Löve & Löve var. *pendulocarpa* (A. Nelson) N. Snow, comb. nov.** *Arabis pendulocarpa* A. Nelson, Bot. Gaz. 30: 192. 1900. *Arabis holboellii* Hornem. var. *pendulocarpa* (A. Nelson) Rollins, Rhodora 43: 446. 1941. TYPE: USA: Wyoming, Yellowstone National Park, June, 1899, A. & E. Nelson 5504 (lectotype: RM [designated implicitly by Rollins 1941: 446], not seen; isotypes: G, NY, US, not seen).

Not all authors have recognized *B. holboellii* var. *pendulocarpa* at this rank, nor agreed that it represents a distinct taxon. It was first recognized by Nelson (1900) at the specific level. However, Weber and Wittmann (1992) placed it in synonymy under *Boechea retrofracta* (R. Graham) Löve & Löve with two other varieties of *Arabis holboellii*, whereas Dorn (2001) considers it a distinct species with at least two varieties. Al-Shehbaz (personal communication 2004) is revising *Boechea* and related genera for a forthcoming volume of *Flora of North America* and has indicated that *B. holboellii* var. *pendulocarpa* ultimately may be treated differently. However, to conform with the work of others in the region who typically recognize members of

this species complex at varietal rank (e.g., Dorn 2001; Welsh et al. 2003) and to be consistent with our checklist (Snow and Brasher 2004), the present combination is necessary.

ACKNOWLEDGMENTS

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A NEW VARIETY OF *ERICAMERIA DISCOIDEA* (ASTERACEAE)
FROM IDAHO AND WYOMING

ROBERT D. DORN

8481 Road 39, Lingle, WY 82223

linglebird@yahoo.com

CHARMAINE H. DELMATIER

29009 Oakland Hills Dr., Georgetown, TX 78628

ABSTRACT

A new variety of *Ericameria discoidea* is described and illustrated. The variety is known from two locations in southeast Idaho and southwest Wyoming. It resembles *E. discoidea* var. *linearis* but has broader leaves that lack the glands that are usually present in var. *linearis*.

Key Words: Idaho, Wyoming, Asteraceae, *Ericameria*.

In September of 1995, the junior author collected a plant specimen in Lincoln Co., Wyoming, that was identified by Ronald Hartman as *Haplopappus macronema* A. Gray var. *linearis* (Rydb.) Dorn [now *Ericameria discoidea* (Nutt.) G. L. Nesom var. *linearis* (Rydb.) G. L. Nesom]. Of the known taxa, this was the closest match, but the senior author suspected that it might represent an undescribed taxon based on apparent leaf differences, a quite different habitat, and its disjunct location from the two varieties of *E. discoidea*.

In March 2002, Alma Winward, U.S. Forest Service Regional Ecologist in Ogden, Utah, showed the senior author a collection that he had made in Bear Lake Co., Idaho, in August of 1985, and asked what it might be. It appeared identical to the collection discussed above.

On 26 July 2002, the senior author visited both collection sites to observe the populations in the field and make additional collections. After comparing these collections with collections of var. *linearis* and contrasting the habitats, he concluded that a new variety is justified.

***Ericameria discoidea* (Nutt.) Nesom var. *winwardii* Dorn & Delmatier, var. nov.**—TYPE: USA, Wyoming, Lincoln Co., ca. 11 mi SW of Kemmerer, 41°42.471'N, 110°43.381'W, 2135 m (7000 ft), 26 Jul 2002, R. Dorn 9393 (Holotype, RM, Isotypes BRY, COLO, MO, NY, IDS).

Differt a var. *linearis* foliis latioribus, latissimis (2.5)3–5 mm latis, brevioribus, dense pubescentibus, et eglandulosis.

Prostrate to erect shrub 0.5–2 dm high; stems densely floccose-tomentose; leaves alternate, petioles very short or mostly lacking, the blades mostly narrowly oblanceolate or elliptic, 6–15 mm long, the largest (2.5)3–5 mm wide, less than six times

as long as wide, loosely floccose-tomentose, eglandular; heads cymose, involucre turbinate to campanulate, 10–12 mm long and 3–4 mm wide, with about 12 bracts in usually two series, these lance-linear or linear-oblancheolate, the outer loosely tomentose, all more or less spinulose-tipped; receptacle naked; rays none; disk flowers 4–9, corolla ca. 9 mm long, the tube ca. 3 mm long, the limb ca. 4.5 mm long, the lobes 1–1.5 mm long and often hairy at least at tip; pappus of 40 or more capillary bristles, 8–9 mm long but with some shorter bristles intermixed, slightly tawny; anthers ca. 3 mm long; style glandular-hairy, ca. 8 mm long excluding the ca. 2–2.5 mm long, linear branches; achenes 5–7 mm long, pilose with ascending hairs

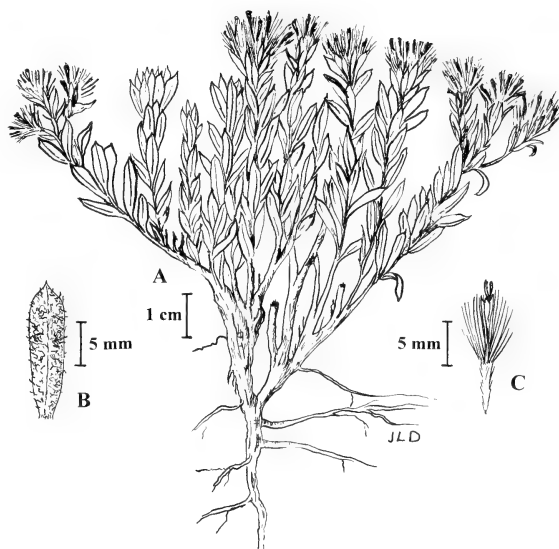


FIG. 1. *Ericameria discoidea* var. *winwardii*. A. Habit. B. Leaf. C. Flower.

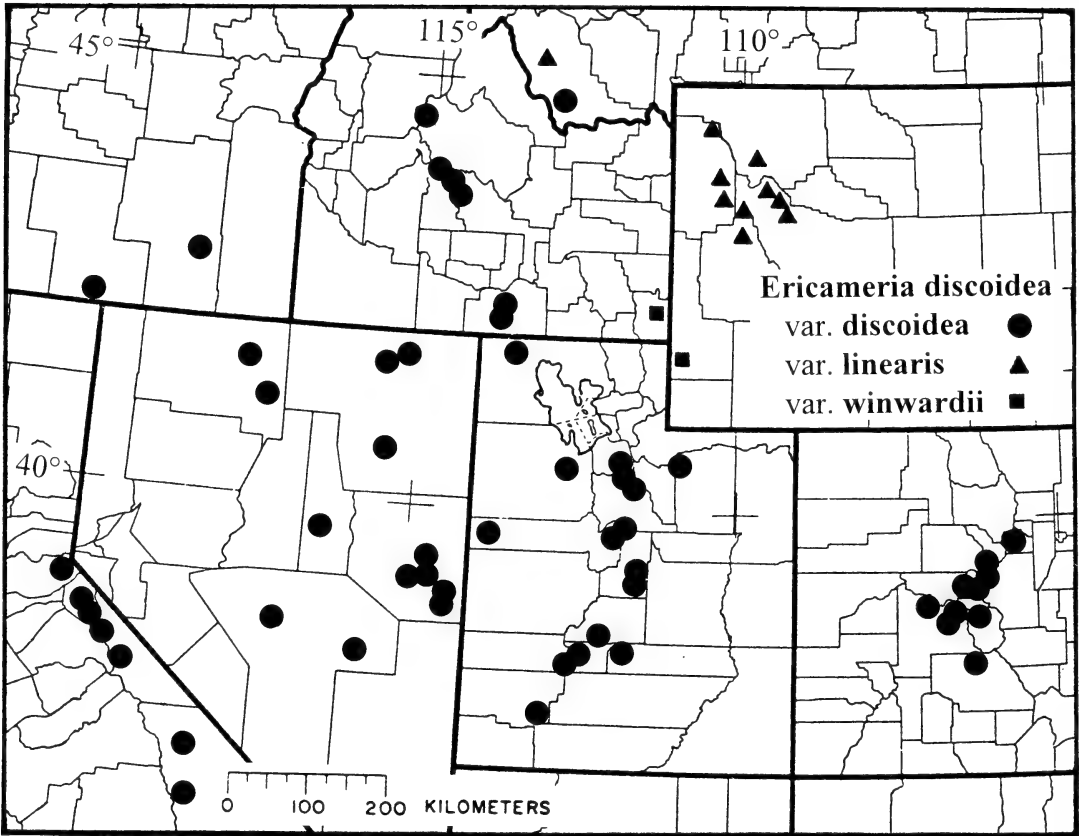


Fig. 2. Distribution of *Ericameria discoidea* varieties based primarily on specimens at RM and USFS. One symbol may represent more than one collection locality.

(Fig. 1). Barren clay-shale slopes and silty clay outwash from whitish outcrop, slopes mostly less than 20°, 2070–2135 m (6800–7000 ft) elevation. Preuss Range, Bear Lake Co., Idaho, and South Fork Twin Creek drainage, southern Lincoln Co., Wyoming.

Paratypes. USA. Idaho, Bear Lake Co.: Snowslide Canyon 10 mi NE of Montpelier, 1 Aug 1985, A. Winward s. n. (Winward Herb.); Crow Creek Road ca. 9 air mi NE of Montpelier, 42°23.757'N, 111°09.348'W, 2070 m (6800 ft), 26 Jul 2002, R. Dorn 9396 (BRY, COLO, MO, NY, RM). Wyoming, Lincoln Co.: ca. 8.2 air mi SW of Kemmerer, T20N R118W S23 E 1/2, 1 Sep 1995, C. Refsdal 7759 (RM).

The three varieties of *Ericameria discoidea* are distinguished as follows.

- 1. Leaves oblanceolate (elliptic), the largest 3–7 mm wide, glandular-pubescent, margins often crisped or wavy; Oregon and California e to sw Montana, Utah, and Colorado var. *discoidea*
- 1. Leaves narrowly oblanceolate to elliptic or linear, the largest 1–5 mm wide, glabrous to glandular-pubescent or floccose-tomentose, margins flat; sw Montana, se Idaho, and w Wyoming

- 2. Leaves mostly linear, six or more times as long as wide, the largest 1–2.5(3) mm wide, glandular-pubescent or rarely glabrous, sometimes floccose-tomentose but still usually glandular; sw Montana and nw Wyoming var. *linearis*
- 2. Leaves narrowly oblanceolate to elliptic, less than six times as long as wide, the largest (2.5)3–5 mm wide, floccose-tomentose and eglandular; se Idaho and sw Wyoming var. *winwardii*

Compared to var. *winwardii*, in the field var. *discoidea* and var. *linearis* are usually taller with the tomentum of the stems contrasting more sharply with the foliage. The leaves of var. *discoidea* are noticeably the broadest with usually wavy or crisped margins while the leaves of var. *linearis* are usually noticeably the narrowest. One might justifiably recognize var. *discoidea* as a species distinct from the other two taxa. Specimens from Fremont County, Wyoming, at RM suggest a closer relationship between var. *linearis* and var. *winwardii*. Varieties *discoidea* and *linearis* usually occur from 2285 to 3960 m (7500 to 13,000 ft) elevation but a few collections are from as low as 1830 m (6000 ft). These are mountain plants often occurring on

coarse soils along streams and lakes. Variety *winwardii* occurs between 2070 and 2135 m in the drier foothills and out into the basins but where the finer clay soils hold moisture and/or where extra runoff provides additional moisture. Their distributions are mapped in Figure 2.

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CONTRIBUTIONS TOWARD A BRYOFLORA OF NEVADA: BRYOPHYTES NEW FOR THE SILVER STATE

JAMES R. SHEVOCK

Department of Botany, California Academy of Sciences, 875 Howard Street,
San Francisco, CA 94103-3098
jshevock@calacademy.org

JOHN R. SPENCE

National Park Service, Glen Canyon National Recreation Area,
Page, AZ 86040-1507

LLOYD R. STARK

Department of Biological Sciences, University of Nevada,
Las Vegas, NV 89154-4004

ABSTRACT

Thirty-four mosses and two liverworts are reported new for the state of Nevada. The moss family Scouleriaceae is new for the state. Genera new for Nevada include: *Blindia*, *Dichodontium*, *Eucladium*, *Molendoa*, *Orthodicranum*, *Porotrichum*, *Pterigynandrum*, *Rhizomnium*, *Roellia* and *Scouleria*.

Key Words: bryogeography, bryophytes, liverworts, mosses, Nevada, new records.

The bryoflora of the state of Nevada is perhaps the least known of all the western states (Lavin 1981; Spence 1988; Shevock 2002). The earliest bryophyte collecting in Nevada can be traced back to Sereno Watson from 1867–1868 during the Geological Surveys of the Fortieth Parallel (Watson 1871). Bryophyte collections obtained by Baker and Nutting near Carson City in 1902 were subsequently published by Cardot and Thériot (1904). Nearly 50 years later the first catalogue of liverworts and mosses was published for the state of Nevada (Clark 1957; Lawton 1958). Lawton's collections obtained during a 1955 expedition to Nevada remained the largest collection of Nevada mosses for over the next 40 years comprised of 520 specimens obtained from 42 collecting sites within 12 of the 17 counties (Lawton 1958). Additional historic herbarium specimens obtained by previous workers are the basis for the Lawton catalogue. A total of 25 liverworts (Clark 1957) and 144 mosses (Lawton 1958) were reported for Nevada. Since that time several other botanists have reported additional taxa as new to the Nevada bryoflora (Lavin 1981, 1982; Rust and Lavin 1986; Heise 2000; Stark and Whittemore 2000; Stark et al. 2002).

We are now in the process of reviewing the herbarium record of bryophytes obtained from Nevada by previous workers. It has recently come to our attention that another large set of Nevada bryophytes was in the personal herbarium of Hugh Nelson Mozingo, who spent a large portion of his academic career at the University of Nevada, Reno. With Mozingo's death in early 2004, his entire herbarium has subsequently been transferred from his

estate to CAS. Many of his Nevada bryophyte collections remain to be labeled and identified. We plan to produce an updated bryophyte catalogue that incorporates all of these data in a future publication. In the interim, we expect to publish at infrequent intervals, in approximately 25–30 species increments, mosses and liverworts as new to Nevada.

Exactly how many bryophytes occur in Nevada remains quite speculative, but at this time, we are of the opinion that the Nevada bryoflora should well exceed 300 taxa. Therefore, nearly 100 additional species are likely to be documented in the state with further collecting. Our projection is based on three primary factors: 1) a review of existing bryophyte inventories from adjacent states and regions (Flowers 1954, 1961, 1973; Hong 1976, 1978, 1979, 1980, 1983, 1986, 1987, 2002; Howe 1989; Christy et al. 1982; Spence 1988; Christy and Harpel 1997; Váña and Hong 1999; Hong and Matthews 2001; Norris and Shevock 2004), 2) an analysis of plant communities and habitats in Nevada that could provide suitable habitat for species within isolated mountain islands in the Great Basin Ranges where no bryophyte collections have been previously obtained from the state, and 3) the number of specimens misidentified in herbaria.

Prior to our collecting efforts, we have located fewer than 1000 Nevada bryophyte collections residing in herbaria obtained between the years 1880 and 2000. During the 2002 field collecting season alone we had more than doubled the number of Nevada bryophyte collections available for study with specimens obtained from every county (Fig.

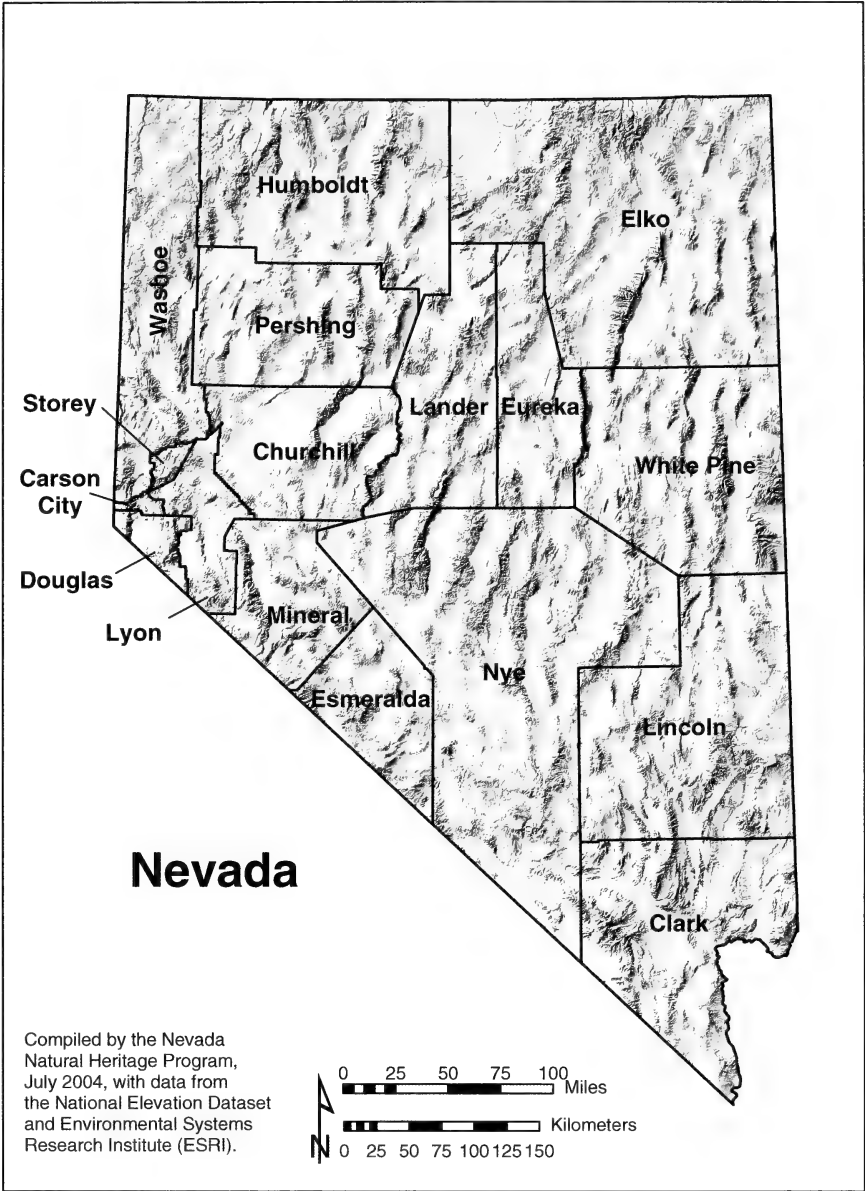


FIG. 1. Location of the 17 counties within the state of Nevada.

1). This publication series format was selected so new state distribution records can be incorporated as they are documented for Nevada into the various treatments for the Bryophyte Flora of North America Project (BFNA).

LIVERWORTS

Mannia fragrans (Balbis) Frye & Clark [Aytoniaceae]

Elko Co.: slopes above Angel Lake, East Humboldt Mts., Humboldt National Forest, *Shevock & Glazer* 22596 (CAS, MO, NY, UC, UNLV, WTU) [determined by Alan Whittemore; con-

firmed by Bill Doyle]. On compacted soil, alpine areas.

Porella cordeana (Hübener) Moore [Porellaceae]

Elko Co.: Pine Creek Canyon near confluence with Jarbidge River, Jarbidge Mts., Humboldt National Forest, *Shevock & Glazer* 22783 (CAS, MO, UC, UNLV) [confirmed by Alan Whittemore and Bill Doyle] and *Shevock & Glazer* 26096, 26102 (CAS, UNLV). On shaded rock wall. Although reported for Nevada by Hong (1983) based on *Lawton* 3053 (TENN), this is the exact same collection number listed as *P. roellii* (COLO) in the same paper. While a mixed collection is possible

where one duplicate has *P. cordeana* and another with *P. roellii*, all of the Lawton Nevada liverwort collections were originally examined by Clark, and she determined *Lawton 3053* as *P. roellii* prior to distribution of duplicates. This record of *Porella roellii* in Nevada was cited as *Lawton 3055* in Clark (1957); however, the correct collection number is in fact *Lawton 3053*. *Lawton 3055* is a collection of *Dicranoweisia*.

MOSSES

***Blindia acuta* (Hedwig) Bruch & W. P. Schimper** [Seligeriaceae]

Elko Co.: Lamoille Canyon above Lamoille Creek off of Ruby Crest Trail to Dollar Lakes, Ruby Mts., Humboldt National Forest, *Shevock & Glazer 22520* (CAS, NY, UC, UNLV), cirque below Greys Peak east of Angel Lake, East Humboldt Mts., Humboldt National Forest, *Shevock & Glazer 22587* (CAS, MO, UC, UNLV) and slopes above Smith Lake north of Angel Campground, *Shevock 25992* (CAS, UBC, UC, UNLV) [confirmed by Wilf Schofield]; **Washoe Co.:** on rocks above high water line of Lake Tahoe, Carson Range, northern Sierra Nevada, Lake Tahoe Basin Management Unit, *Shevock 22048* (CAS, UNLV) [confirmed by Dan Norris]. On rocks, seasonally wet.

***Brachythecium albicans* (Hedwig) Bruch & W. P. Schimper** [Brachytheciaceae]

Douglas Co.: South Fork Daggett Creek above Highway 371, Carson Range, northern Sierra Nevada, Toiyabe National Forest, *Shevock 22143* (CAS, UC, UNLV) [determined by Dan Norris]. On soil and litter.

***Brachythecium asperillum* (C. Müller Hal.) Sullivant** [Brachytheciaceae]

Carson City Co.: Clear Creek Canyon just south of Highway 50, Carson Range, northern Sierra Nevada, Toiyabe National Forest, *Shevock 21968* (CAS, UC, UNLV); **Eureka Co.:** Jackass Creek, Roberts Mts., *Nachlinger & Tiehm 2436* (CAS, UC, UNLV) and North Fork Allison Creek about 2.5 miles northeast of South Fork Pass, Monitor Range, Toiyabe National Forest, *Shevock & Glazer 22376* (CAS, UC, UNLV); **Washoe Co.:** southwest of Truckee Meadows north of Highway 431 along Whites Creek, *Nachlinger & Taylor 2458* (CAS, UC, UNLV), Marlette Reservoir Creek east of Highway 28, Carson Range, northern Sierra Nevada, Lake Tahoe Basin Management Unit, *Shevock & Durham 21971 & 21977* (CAS, UC, UNLV) [determined by Dan Norris]. On soil, frequently at base of boulders and along stream banks.

***Brachythecium plumosum* (Hedwig) Bruch & W. P. Schimper** [Brachytheciaceae]

Esmeralda Co.: Morris Creek, north base of Boundary Peak, White Mts., Inyo National For-

est, *Shevock & Glazer 22293* (CAS, UNLV) [determined by Dan Norris]. On rocks along stream banks.

***Brachythecium reflexum* (Starke in Weber & D. Mohr) Bruch & W. P. Schimper** [Brachytheciaceae]

White Pine Co.: Sharp Creek, Antelope Range, *Nachlinger 2479* (CAS, UC, UNLV) [determined by Dan Norris]. On rocks along stream banks.

***Brachythecium salebrosum* (Weber & D. Mohr) Bruch & W. P. Schimper** [Brachytheciaceae]

Elko Co.: Mahoney Forest Service Station about 1 mile north of the community of Jarbidge, Jarbidge Mts., Humboldt National Forest, *Howell 35* (CAS, UNLV); **Nye Co.:** Strozzi Ranch Site south of Wahguyhe Peak, Grapevine Mts., Death Valley National Park, *Shevock & York 21682* (CAS, UC, UNLV) [determined by Dan Norris]. On litter and soil.

***Brachythecium starkei* (Bridel) Bruch & W. P. Schimper** [Brachytheciaceae]

Douglas Co.: Pipeline Canyon, eastern slope of Pine Nut Mts., *Shevock, Durham, & Tonenna 22004* (CAS, UNLV) [determined by Dan Norris]. On rocks along stream banks.

***Dichodontium pellucidum* (Hedwig) W. P. Schimper** [Dicranaceae]

Elko Co.: Jarbidge River at Lower Bluster Campground, Jarbidge Mts., Humboldt National Forest, *Shevock & Glazer 22726* (CAS, UC, UNLV) [determined by Dan Norris]. On rocks in splash zone of river.

***Didymodon brachyphyllus* (Sullivant in Whipple) Zander** [Pottiaceae]

Mineral Co.: Anchorite Hills just east of Anchorite Pass, Highway 359, Wassuk Range, Toiyabe National Forest, *Shevock 22112* (CAS, MO, UC, UNLV); **Nye Co.:** Phinney Canyon northeast of Wahguyhe Peak, Grapevine Mts., Death Valley National Park, *Shevock, York, & Davis 23697* (CAS, MO, UC, UNLV). [determined by Richard Zander]. On rock crevices and underhangs of boulders.

***Didymodon nicholsonii* Culmann** [Pottiaceae]

Douglas Co.: Pipeline Canyon, eastern slope of Pine Nut Mts., *Shevock, Durham, & Tonenna 22002* (CAS, MO, UC, UNLV) [determined by Richard Zander]. On soil and litter.

***Eucladium verticillatum* (Hedwig in Bridel) Bruch & W. P. Schimper** [Pottiaceae]

Clark Co.: Nickel Creek, Virgin Mts., *Shevock, Glazer, Spence, & Nelson 23647* (CAS, UC, UNLV). On wet soil or rock walls of alkaline springs and seeps.

***Fissidens crispus* Montagne** [Fissidentaceae]

Washoe Co.: Highway 28 between Incline Village and Crystal Bay, Lake Tahoe Basin Management

Unit, *Shevock* 22670 (CAS, PAC, UC, UNLV) [confirmed by Ronald Pursell]. On shaded soil at base of boulders.

***Fontinalis neomexicana* Sullivant & Lesquereux** [Fontinalaceae]

Washoe Co.: west end of Big Meadow, Carson Range north of Lake Tahoe, *Lavin, Mozingo, & Edgington s.n.* (NY); **White Pine Co.:** Baker Creek at trailhead to Baker Lake above Baker Creek Campground, Great Basin National Park, *Shevock, Glazer, & Clifton* 23242 (CAS, MO, NY, UC, UNLV, WTU) and *Mozingo* 74-44c (NY), 75-095 (NY). Attached to rocks submerged in creek.

***Hypnum revolutum* (Mitten) Lindberg var. *ra-vaudii* (Boulay) Ando** [Hypnaceae]

Eureka Co.: White Sage Canyon, Monitor Range, Toiyabe National Forest, *Shevock & Glazer* 22388 (CAS, UBC, UNLV); **Lander Co.:** Toquima Cave area, Toquima Range, Toiyabe National Forest, *Shevock & Glazer* 22358 (CAS, UBC, UNLV) [determined by Wilf Schofield]. On rock walls.

***Molendoo sendtneriana* (Bruch & W. P. Schimper) Limpricht** [Pottiaceae]

Clark Co.: Red Rock Canyon BLM National Conservation Area, *Allen* 21895 (MO). On moist soils and rocks.

***Orthodicranum tauricum* (Sapehin) Smirnova** [Dicranaceae]

Douglas Co.: South Fork Daggett Creek off of Highway 371 below Daggett Saddle, Carson Range, northern Sierra Nevada, *Shevock* 22147 (CAS, UC, UNLV); **Washoe Co.:** Marlette Reservoir Creek east of Highway 28, Lake Tahoe Basin Management Unit, *Shevock & Durham* 219737 (CAS, UC, UNLV). At base of conifer trunks or rotten logs, primarily on *Calocedrus decurrens*.

***Orthotrichum affine* Schader ex Bridel** [Orthotrichaceae]

Douglas Co.: South Fork Daggett Creek above Highway 371 (Kingsbury Grade) about 4.5 miles below Daggett Saddle, Carson Range, northern Sierra Nevada, *Shevock* 22152 (CAS, UNLV) [determined by Dan Norris]. On trunk of *Abies concolor*.

***Orthotrichum flowersii* Vitt** [Orthotrichaceae]

Nye Co.: Phinney Canyon, Grapevine Mts., Death Valley National Park, *Shevock, York, & Davis* 23671 (CAS, SIU, UC, UNLV) and Strozzi Ranch Site, south of Wahguyhe Peak, Death Valley National Park, *Shevock, York, & Davis* 21581 (CAS, UNLV) [determined by Dale Vitt and Dan Norris]. While this species is generally corticolous, the Death Valley occurrences are on a vertical rock walls.

***Orthotrichum lyellii* W. J. Hooker & Taylor** [Orthotrichaceae]

Clark Co.: Virgin Peak Ridge, Virgin Mts., *Shevock & Spence* 23657 (CAS, UC, UNLV); **Douglas Co.:** eastern slope of Pine Nut Mts., *Shevock, Durham, & Tonenna* 23657 (CAS, UC, UNLV); **Nye Co.:** Phinney Canyon, Grapevine Mts., Death Valley National Park, *Shevock & York* 23704 (CAS, SIU, UNLV) [determined by Dale Vitt] and Strozzi Ranch Site, south of Wahguyhe Peak, Grapevine Mts., Death Valley National Park, *Shevock, York, & Davis* 21593 (CAS, UNLV). On trunks of *Quercus* and rock walls.

***Orthotrichum papillosum* Hampe** [Orthotrichaceae]

Douglas Co.: Genoa Creek above town of Genoa, Carson Range, northern Sierra Nevada, Toiyabe National Forest, *Shevock & Durham* 21985 (CAS, MO, UC, UNLV) [determined by Dan Norris]. On trunks of *Alnus* in riparian woodland.

***Orthotrichum pumilum* Swartz** [Orthotrichaceae]

Elko Co.: Forest Road 748 near Camp Draw Trailhead, Jarbidge Mts., Humboldt National Forest, *Shevock & Glazer* 22688 (CAS, UC, UNLV) and along Jarbidge River at Lower Bluster Campground, *Shevock & Glazer* 22727 (CAS, UC, UNLV) [determined by Dan Norris]. On rocks and boulders.

***Orthotrichum shevockii* Lewinsky-Haapasaari & Norris** [Orthotrichaceae]

Carson City Co.: Voltaire Canyon north of Highway 50, Carson Range, northern Sierra Nevada, Toiyabe National Forest, *Shevock* 21948 (CAS, MO, UC, UNLV) and below Secret Harbor Vista Point off of Highway 28, Lake Tahoe Basin Management Unit, *Shevock* 22038 (CAS, UC, UNLV) [confirmed by Dan Norris]. On crevices and underhangs of granitic rocks and boulders.

***Orthotrichum speciosum* Nees in J. W. Strum** [Orthotrichaceae]

Washoe Co.: slope above Highway 28 between Incline Village and Crystal Bay, Carson Range, northern Sierra Nevada, Lake Tahoe Basin Management Unit, *Shevock* 22662 (CAS, UC, UNLV). [determined by Dan Norris]. On rocks and boulders.

***Orthotrichum spjutii* Norris & Vitt** [Orthotrichaceae]

Lander Co.: Highway 722 east of Carroll Summit, Desatoya Mts., *Shevock & Glazer* 22408 (CAS, UC, UNLV) [determined by Dan Norris]. On rocks and boulders.

***Plagiomnium cuspidatum* (Hedwig) T. Koponen** [Mniaceae]

Elko Co.: below Snowslide Gulch, Jarbidge River, Jarbidge Mts., Humboldt National Forest, *Howell* 6 (CAS, UNLV); **Esmeralda Co.:** Indian Creek 6.5 miles west of Highway 264, White Mts., Inyo

National Forest, *Shevock, Glazer, & Laeger* 21833 (CAS, UC, UNLV); **White Pine Co.:** Lehman Creek at Lower Lehman Creek Campground, Snake Range, Great Basin National Park, *Shevock* 17775 (CAS, UC, UNLV) [determined by Dan Norris]. On shaded and moist soil and litter, generally about springs and stream banks.

***Polytrichum piliferum* Hedwig** [Polytrichaceae]

Elko Co.: west side of Angel Lake, East Humboldt Mts., Humboldt National Forest, *Shevock & Glazer* 22556 (CAS, UC, UNLV, WTU), Lamoille Canyon, Lamoille Creek along Ruby Crest Trail to Dollar Lakes, Ruby Mts., Humboldt National Forest, *Shevock & Glazer* 22493 (CAS, UC, UNLV), Jarbidge River at Lower Bluster Campground, Jarbidge Mts., Humboldt National Forest, *Shevock & Glazer* 22737 (CAS, NY, UC, UNLV); **Mineral Co.:** east slopes of Mount Grant, Wassuk Range, Toiyabe National Forest, *Nachlinger & Tiehm* 2449 (CAS, MO, UC, UNLV). On dry soil among rocks.

***Porotrichum bigelovii* (Sullivant) Kindberg** [Neckeraceae]

Clark Co.: Lost Creek, BLM Red Rock Canyon National Conservation Area, *Shevock & Stark* 23975 (CAS, UC, UNLV). Shaded seep of rock wall.

***Pterigynandrum filiforme* Hedwig** [Pterigynandraceae]

Carson City Co.: Highway 28 just south of the Washoe County line below Vista Point north of Secret Harbor, Carson Range, northern Sierra Nevada, Lake Tahoe Basin Management Unit, *Shevock* 22052 (CAS, MO, UC, UNLV). At base of conifer trunks.

***Rhizomnium pseudopunctatum* (Bruch & W. P. Schimper) T. Koponen** [Mniaceae]

Elko Co.: Stringer of Bear Creek paralleling Forest Road 748 north of Bear Creek Summit, Jarbidge Mts., Humboldt National Forest, *Shevock & Glazer* 22700 (CAS, UC, UNLV) and 22712 (CAS, UC, UNLV) [confirmed by Dan Norris]. On moist and shaded soil and litter of stream banks.

***Roellia roellii* (Brotherus in Röhl) Andrews ex H. Crum** [Mniaceae]

Elko Co.: along Forest Road 748 north of Bear Creek Meadow toward Jarbidge River, Jarbidge Mts., Humboldt National Forest, *Shevock & Glazer* 22721 (CAS, MO, UC, UNLV), Forest Trail 106 at Sawmill Creek, Jarbidge Wilderness, *Shevock, Glazer, & Howell* 26109 (CAS, MO, NY, UC, UNLV) and west of Bear Creek Summit toward Coon Creek, *Shevock & Glazer* 26083 (CAS, UC, UNLV). On shaded soil and litter in forest understory.

***Schistidium cinclidodontum* (C. Müller Hal. in Röhl) B. Bremer** [Grimmiaceae]

Nye Co.: Above Strozzi Ranch Site south of Wahguyhe Peak, Grapevine Mts., Death Valley National Park, *Shevock & York* 21686 (CAS, KRAM, UC) [confirmed by Ryszard Ochyra].

Washoe Co.: slopes west of Pyramid Lake, *Tonnenna* 5 (CAS, KRAM, UNLV) [confirmed by Ryszard Ochyra]. On rock slabs of intermittent stream channels and rivulets.

***Scouleria aquatica* W. J. Hooker in Drummond** [Scouleriaceae]

Elko Co.: Lamoille Creek adjacent to Ruby Crest Trailhead, Lamoille Canyon, Ruby Mts., Humboldt National Forest, *Shevock & Glazer* 22473 (CAS, UC, UNLV). On rocks in splash zone of creek or on boulders seasonally submerged.

***Sphagnum squarrosum* Crome** [Sphagnaceae]

Elko Co.: Copper Basin Bog, south of Coon Creek Summit and east of Copper Mountain, Jarbidge Mts., Humboldt National Forest, *Howell* 11 (CAS, UNLV) [confirmed by Richard Andrus] and Cherry Creek about 5 air miles south of the Idaho/Nevada state line, *Howell* 38 (CAS, UNLV) [determined by Richard Andrus]. Fen habitats.

***Sphagnum subsecundum* Nees in Sturm** [Sphagnaceae]

Washoe Co.: fen above Ophir Creek and about 1 mile below Tahoe Meadows, Carson Range, northern Sierra Nevada, Toiyabe National Forest, *Matson* 975 (CAS) [determined by Richard Andrus].

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ABORIGINAL DISTRIBUTION OF *QUERCUS LOBATA* WOODLAND ON THE KAWEAH RIVER DELTA, CALIFORNIA

KHALED J. BLOOM¹

CONRAD J. BAHRE

Department of Land, Air, and Water Resources, University of California,
Davis, CA, 95616

ABSTRACT

In 1853 the Kaweah River delta (western Tulare County) was one of California's richest natural habitats, the so-called Giant Oak Forest its leading feature. By 1920 this unique formation was completely cleared, drained, and leveled for intensive agricultural use. We present a reconstruction of the 1853 vegetation pattern based on U.S. General Land Office survey notes.

Key Words: California oak woodlands, deforestation, land use impacts, riparian zones, San Joaquin Valley.

Historically, the delta of the Kaweah River comprised one of California's most productive riparian areas, including the San Joaquin Valley's most extensive stands of *Quercus lobata*, Neé (Fagaceae). With associated belts of grassland and tule marsh, the oak woodland of this inland delta had supported what Cook (1955) identified as the heaviest concentration of aboriginal population in California, "or possibly even north of the Valley of Mexico." Agricultural settlement after 1853 brought gradual clearing of wooded areas for cultivation, along with heavy livestock grazing and diversion of water for drainage and irrigation. The general thinning and deterioration of the oak woodland was noted as early as 1878 (Anonymous 1878); by 1903 only fragments of it survived (Anonymous 1903). By 1921 some 90 percent of the Kaweah's surface flow was diverted and groundwater was subjected to heavy pumping (California Department of Public Works 1922). A soil survey team working here in 1935 attributed the death of the remaining old-growth oaks to abrupt dewatering of the soil profile (Storie et al. 1940).

The aboriginal landscape of the Kaweah delta was obliterated before it was ever mapped; subsequent cartographic depictions were based on little more than guesswork (Preston 1982). In 1853–1854 the area was still public domain and largely free of agricultural disturbance (Blake 1858; Leonard 1928). Surveyors employed by the U.S. General Land Office were establishing the crosshatch of townships and sections that would be the basis of future property description (Gibbes 1854). Their instructions required them to note the vegetation along each linear mile (1.6 km) of the survey grid. These firsthand observations along a permanent cadastral framework constitute a recognized baseline for the evaluation of postsettlement vegetation

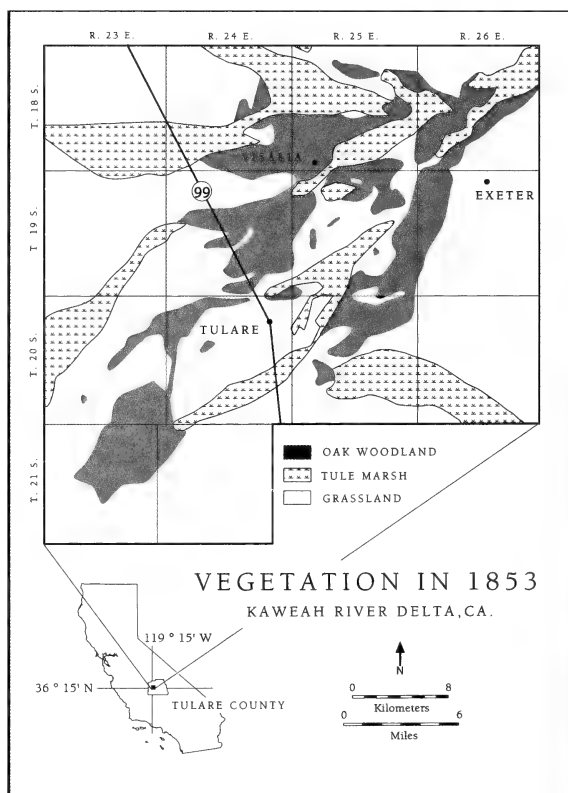


FIG. 1. *Quercus lobata* (valley oak) woodland and associated vegetation types of the aboriginal Kaweah delta, in relation to the U.S. public land survey township grid (U.S. General Land Office 1853–1854), to the modern cities of Visalia, Tulare, and Exeter, and to the route of modern California State Highway 99. The North (Main) Branch of the Tule River joins the delta system from the southeast.

¹ Author for correspondence, e-mail: kjbloom@ucdavis.edu

change (Whitney and DeCant 2001). We followed the surveyors' traverse along 1700 km (1056 mi) encompassing 14 contiguous townships, approximately 130,000 ha (504 sq mi). We transcribed the surveyors' observations from their field notes to 15-minute USGS topographic quadrangles, then consolidated the information on a single sheet (Fig. 1).

The oak stands were irregularly distributed around and between the delta's wide-spreading sloughs, in the overall form of a vast scalene triangle. The impressions of early visitors were limited by line of travel and line of sight, which gave rise to widely varying estimates of the original extent of the woodland. The very liberal estimate of 100,000 ha (400 sq mi) was published by Jepson (1910) and became embedded in the literature (e.g., Griffin 2000). In fact, Hilgard's (1884) estimate of 20,000 ha (75–80 sq mi) was most accurate. One early characterization of this landscape as a complex of "wooded islands" was rather apt (Cronise 1868). However, we have not found any clear-cut physiographic explanation for the spatial pattern of the oak "islands." They do not correspond to any soil series delineated in the recent soil survey of the area (Wasner and Arroues 2000), nor do topographic maps indicate a consistent association with any facet of local relief. The natural hydrologic pattern, both winter-spring flooding and summer-fall subirrigation, has been altered so profoundly for so long (Grunsky 1898) that no comparative assessment can be made.

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REVIEWS

The Valley of the Second Sons. Edited by William Weber. 2004. Pilgrims Process, 4066 Niblick Dr., Longmont, CO. 567 pp. Softcover \$39.95. ISBN 0-9710609-9-1.

At the end of an enviable scientific career, Theodore Dru Alison Cockerell (1866–1948), distinguished entomologist and longtime zoology professor at the University of Colorado, had generated a record bibliography of 3904 published works. Now in a hefty compendium, Dr. William A. Weber, retired curator of the University of Colorado Herbarium, has added to this bibliography hundreds of Cockerell's early personal letters written during 1887–1890. These epistles, sent from an isolated mountain valley in the southern Colorado Rockies to England, were for fellow naturalist Frederic Fenn and his sister Annie, whose father was author George Manville Fenn. Although Theo and Annie were in love, George objected to young Cockerell because of his socialistic ideas and weak constitution, and for months the couple could only communicate through Frederic.

At twenty years of age Londoner Theo, diagnosed with consumption, had repaired to the Wet Mountain Valley for its restorative climate. He joined a congregation of kindred British health seekers as well as adventurous young Englishmen and other settlers in the environs of West Cliff village on the eastern flank of the Sangre de Cristo Range. The vale was informally known as "the Valley of the Second Sons" because of its multitude of British expatriates.

Cockerell's chatty correspondence, often written daily, usually wordy, occasionally including sketches, and always more enthusiastic after a mail delivery from London, dealt in part with the routine of frontier life: repairing cabins, finding lost horses, planting vegetables. But more interesting were the many natural history observations, commentaries on newspapers and magazines that Cockerell received, discussion of books which Theo and the Fenns were reading, the programs of the local natural history and literary societies Cockerell had founded, his diversity of correspondents, descriptions of acquaintances, the mountain valley social life, exchanges on politics, women's affairs, love and marriage, housekeeping, illness, employment, evolution, religion. . . .

The Wet Mountain Valley was a mining district in decline, but Cockerell's letters represent rich historical "mother lodes" waiting to be mined. From these one could compile the first springtime arrival dates of local birds, European weeds which Cockerell encountered in frontier Colorado, good books and authors worth exploring today, a roster of Wet

Mountain Valley's butterflies and mammals, a comparison between fungi of England and Colorado, winter weather, topics of frontier debating societies, mountain meal menus, and informative sidelights on who was doing what in America and Europe.

Cockerell and his second wife Wilmatte (Annie died in 1893) are considered by Coloradoans as "their very own" and are buried in Boulder's Columbia Cemetery. Yet commencing with his retirement in 1934, the Cockerells typically wintered in San Diego, California, and Theo died there in a local hospital from a stroke on the morning of January 26, 1948. During the six decades after convalescent Cockerell's adventures in "the Valley of the Second Sons," he actually had many relationships with the Golden State. He supposedly first visited in 1901, and during winter retirement there he continued natural history research, especially on the coastal islands. During the war years, Theo served as curator of the Palm Spring's Desert Museum.

But already by 1888, the California connection had been made, as letters to the Fenns reveal. In October of 1888 Cockerell began a trial subscription to Charles Orcutt's *West American Scientist*, published in San Diego, and he asked to write for the "not remarkable" magazine. His first article, "Notes from Colorado," appeared at the end of that year. The next July, Orcutt invited him to become Associate Editor, and by September Cockerell was busy preparing an index to the publication's first four volumes. Another Californian connection appeared in an April 14, 1889 letter, with Theo relating that Mrs. Freer, a farm wife taking drawing lessons with him, told Cockerell that as a girl she attended a Canyon City school "kept" by Townshend Brandegee. Ah, yes, reflected Cockerell, Brandegee "was the first to collect plants in the district."

Of more lasting California import was the membership application for Cockerell's newly created Colorado Biological Association received in April, 1889, from a Denver substitute teacher and botanist named Alice Eastwood. Then on June 16, Theo heard that Miss Eastwood was at the hotel in West Cliff, but when he visited there, "she was not to be found." Undaunted, T.D.A. finally tracked her down at the hostel by 7 p.m., and they chatted for over two hours: "Certainly I have never enjoyed any talk so much since I left England." Indeed he entirely forgot about supper. The next day, in a letter to his sweetheart Annie Fenn, he reported running into Miss Eastwood in the morning with her fresh collection of flowers, which they examined together. The afternoon "was devoted to a pleasant ramble down the creek," and Eastwood told him of botanizing atop Gray's Peak with biogeographer

Alfred Russel Wallace, with whom, incidentally, Theo had been corresponding. The morning of the 19th, Alice and Theo collected some plants for his botany class of three girls. Then Alice, Theo, and Mrs. Cusack (Cockerell's intellectual and "spiritual" English friend) put their heads together over their herbarium collections. The next day, Alice and Theo "searched again for specimens" in the field, and he, Eastwood, and Mrs. Cusack "sat up late looking over the herbarium." On Miss Eastwood's next to last day, she and Theo talked until ten in the evening about her flower collecting and then discussed William Morris' *Aims of Art*. Again Cockerell missed supper. To Annie, Cockerell wrote that he "Should like to introduce her [Eastwood] to you. I am sure you would like her." On June 22, with T.D.A. at the station "to see her off," 31-year old Alice Eastwood departed by the morning train for Denver and on to southwest Colorado.

Two weeks later, Theo received what he considered "an extraordinary epistle" from Miss Eastwood, predicting that he was destined "to do lots of good in the world" and should take care of his health. When Alice later left Denver to camp out with the "Mesa Verde" Wetherills in the Southwest, she planned to visit the Wet Mountain Valley once more, but unfortunately the train tracks had been washed out.

Cockerell and Eastwood would not meet again in Colorado, but Theo saw to it that Alice replaced him as Colorado Biological Association secretary. Winter and spring of 1890 Alice was in Florida with an ill friend. Theo and Alice exchanged letters, and Eastwood shipped him a box of colorful *Donax* clam shells. In June when Alice, bound again from Denver to Wetherill's Alamo Ranch, contemplated visiting Cockerell, he had already left for England. That December Miss Eastwood accompanied a handicapped friend to San Diego, and in exactly two years she was appointed joint curator of botany with Townshend Brandegee's wife Katharine for the California Academy of Sciences. Decades later Theo and Alice met for lunch at the Academy, and in his *Recollections*, Cockerell reflected that he and Alice in 1889 "could not know that we should be the last survivors of those then actively concerned with Colorado natural history."

Perusing Theodore Cockerell's letters in William Weber's new book will transport one back to that "Valley of the Second Sons," looking forward to the next mail delivery. Readers of this magnum opus will agree with Alice Eastwood, who wrote of Cockerell, "I have learned much from you."

—RICHARD G. BEIDLEMAN, University and Jepson Herbaria, University of California, Berkeley, CA 94720-2465.

REVIEWS

Burning Questions: America's Fight with Nature's Fire. By David Carle. 2002. Praeger Publishers, Westport, CT. 298 pp. \$26.95. ISBN 0-2759737-1-9.

With recent catastrophic wildfires forcing another re-examination of the nation's fire management policies, David Carle's new book, *Burning Questions, America's Fight with Nature's Fire*, provides a timely, historical overview of the U.S. government's forest fire suppression efforts and the controversial practice of prescribed burning. For those unfamiliar with the story, Carle does an excellent job introducing the subject and describing the individuals involved. He weaves a fascinating story of how twentieth century fire management evolved. It is not, however, a dispassionate examination of people and events. Within the first few pages it becomes clear Carle intends to reveal how wrong-headed fire suppression policy has been during the past one hundred years, lionizing advocates of prescribed burning while deriding its opponents. Using the career of University of California fire ecologist Harold Biswell as a basic framework, Carle portrays the early U.S. Forest Service as an entrenched bureaucracy unwilling to listen to facts in their single-minded crusade to prevent forest fires. Biswell and other proponents of using fire as a management tool are described as quiet crusaders patiently continuing their research while resisting political pressure to do otherwise and not interfere with professional foresters trying to protect the country's natural resources.

The book uses extensive quotes from articles and personal letters to detail the historical debate on the proper role of fire in the nation's forests. The first few chapters describe early resource managers viewing trees as an agricultural crop needing protection from flames and ignoring evidence that fire is often a positive force in maintaining the health of some forests. The use of "light burning" or "Indian forestry" (the original terms for prescribed burning) to reduce forest undergrowth were seen as primitive and misguided. Trees needed to be protected. When three million acres burned in Idaho and Montana in 1910 during a ten-day spell of high winds and low humidity, killing 85 people, renewed political energy was directed toward coordinating fire suppression efforts between state and federal agencies. In 1927 a significant effort began to halt the annual burning practices of rural southern farmers in longleaf pine stands. During World War II, the government turned up the public relations campaign by brilliantly exploiting the dramatic images of the fire scene in Walt Disney's movie "Bambi" and inventing a new fire-fighting

mascot named Smokey Bear. By the early 1950's fire was successfully demonized as a truly evil force. It became the patriotic duty of all citizens to do their share to prevent forest fires. The phrases "Don't Play with Matches" and "Only You" were etched into the public's consciousness, representing one of the most successful advertising efforts in history.

It is now recognized that many land managers did not fully understand the important role fire can play in many forest ecosystems. Our success in excluding fire from some forests was a mistake and the negative consequences have been documented (Agee 1993), the most obvious being fuel buildup on the forest floor. The increased density of both dead and living biomass creates explosive conditions often leading to massive crown fires and extensive loss of life and property. Carle's continual "I told you so" perspective does become distracting at times, but the story he tells still provides an excellent description of how difficult it can be to change public policy in the face of bureaucratic inertia and personal agendas.

Unfortunately, Carle makes the same mistake Harold Biswell did when attempting to apply prescribed burning practices for forests too broadly; both have failed to understand the role of fire in California chaparral, viewing any dense growth of shrubbery as unnatural and in need of removal. In Carle's view, both overgrown forests and old growth chaparral are artifacts of modern fire suppression practices and need to be dealt with in the same manner, preferably by burning. The application of this "one-size-fits-all" model is especially curious since Carle clearly understands the distinctions between different types of forests, each with its own ecological requirements. After discussing the Yellowstone fires of 1988, he wrote, "Not all trees and not all forests are alike, and their relationship to fire form part of that variability. Lodgepole pine forests occupying most of the Yellowstone plateau are adapted to a different fire regime than lower elevation forests. . . ." Commenting on the complexity of the problem he writes later that "All of this can be confusing to people; it would be much simpler if every forest habitat followed one simple pattern."

Carle's misunderstanding of chaparral fire regimes is important because chaparral is California's most fire prone plant community. It is also the most extensive native vegetation type in the state. By repeating one of the more commonly held myths that "fire is necessary to keep the chaparral ecosystems vigorous and productive," Carle adds credence to a discredited idea and reveals a degree of unfamiliarity with current research. The notion that

chaparral needs to burn originated in the mid 1900's with studies concluding animal forage is reduced as chaparral stands age (Biswell et al. 1952). Since measurements were restricted to vegetation below 1.5 meters, above which deer could not reach, the research ignored the upper canopy where most growth occurs. Hanes (1971) gave further legitimacy to the idea by giving it a name; chaparral stands over sixty years old were "decadent" or "senile." More recent studies have failed to support this conclusion by showing no reduction in productivity in chaparral stands nearly a century old (Larigauderie et al. 1991) and increasing, not decreasing, levels of living biomass with chaparral age (Specht 1969; Rundel and Parsons 1979; Schlesinger and Gill 1980).

In reference to whether or not successful fire suppression efforts have created unnatural, dangerous fuel conditions in chaparral, Carle cites only those papers supporting prescribed burning in brushlands and ignores a significant amount of evidence questioning the usefulness of the practice (Dunn 1989; Keeley et al. 1999; Zedler and Seiger 2000). In particular, the Baja fire mosaic model, based on satellite imaging of southern California and northern Baja, is cited as proof chaparral fires remain small and stop at previous burn scars if they have been allowed to burn naturally in the past (Minnich and Chou 1997). No effort is made to question the model's basic assumptions that Baja and southern California landscapes provide valid comparisons, fire perimeters can be accurately determined by the methods described, and that older chaparral is more likely to burn than young chaparral. This is particularly ironic since descriptions of California's most destructive fires, all driven by extreme wind conditions rather than fuel type, are detailed in the same chapter.

The more recent Cedar fire in San Diego County, California in October 2003 demonstrated the relative importance of wind compared to fuel age by burning through multiple age classes of chaparral during dry, Santa Ana wind conditions. An eight-kilometer long, two to four kilometer wide stand of seven year old, chamise chaparral was unable to stop the fire front before it reached and burned several hundred homes in the community of Scripps Ranch and jumped a sixteen-lane interstate highway (Halsey unpublished data). According to prescribed burn proponents, the fire should have terminated in this area and gone no further. However, under severe wind conditions, previous burn scars and age class mosaics are not helpful in preventing the spread of wildfires because flying embers can travel up to a mile or more. Research analyzing fire histories up to 85 years in length from ten large shrubland landscapes between central California to Baja have also demonstrated that hazard of burning shows little relation to fuel age and time since the last fire (Moritz 2003; Moritz et al. 2004). Further

discussion of this subject can be found in Keeley and Fotheringham (2003).

Carle's intense focus on burning vegetation to help solve the danger of wildfire has also overshadowed the other half of the equation, community planning. Although wood shingles, narrow roads, and hillside homes were acknowledged as major contributing factors in the devastating 1991 Oakland/Berkeley Hills fire, the question of future design to help prevent another catastrophe was inadequately addressed. Californians live in a highly fire-prone environment and need to understand vegetation management is only part of an overall strategy to reduce fire risk. To his credit, Harold Biswell accurately predicted what happened in the 1991 fire several years before. His warnings were unfortunately ignored and remain so today by those living in nearby communities.

When Carle returns to discussing forests, however, he is clearly on familiar ground and provides excellent summaries of both the 1988 Yellowstone and 2000 Cero Grande, New Mexico fires as well as the political fallout. Quoting Bruce Kilgore of the National Park Service, Carle pinpoints the end result of the government's successful campaign to convince its citizens that all forest fires are evil. Referring to the political and public outcry after the Yellowstone fires, Kilgore saw "a breakdown in public understanding of the natural role of fire in wildlands, and particularly in our ability to communicate through television, radio, and the press with the public about that role in Yellowstone and elsewhere."

In stressing the need to return fire back to forest ecosystems, Carle makes it very clear that focusing on just reducing fuels is the wrong approach. Fire must be reintroduced because it "moves across a landscape with random variability that transforms all of its impacts into ecosystem biodiversity for soil, plants, and animals, that makes every forest far 'more than the sum of its cellulose.'" This further complicates the use of logging to accomplish fuel reduction. Not only does timber harvesting take the largest trees and leave behind smaller, kindling-sized material, but also fails to support the necessary steps in creating a healthier forest through the reintroduction of fire.

The costs of excluding fire in certain ecosystems continue to be high as are the costs of failing to understand the risks we take when living within fire-prone environments. Prescription burning is definitely an important tool, but only when used in the appropriate natural community. As Carle writes in his final chapter, "We need to embrace a different, older relationship that humanity once had with fire. To recognize that fires are as essential to most of our wildlands as predators are essential to prey."

In recognizing the proper role of fire, it is also our responsibility to make sure it is applied in a manner consistent with the preservation of healthy communities, both human and wild.

—RICHARD W. HALSEY, Southern California Chaparral Field Institute, P.O. Box 545, Escondido, CA 92033. naturalist@californiachaparral.com.

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ABORIGINAL DISTRIBUTION OF *QUERCUS LOBATA* WOODLAND ON THE KAWEAH
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Richard G. Beidleman.....
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Editor—DR. JOHN HUNTER
c/o UC Davis Herbarium/Center for Plant Diversity
Plant Biology
One Shields Avenue
University of California Davis
Davis, CA 95616
johnhunterca@sbcglobal.net

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NET PRIMARY PRODUCTIVITY OF A WESTERN MONTANE RIPARIAN FOREST: POTENTIAL INFLUENCE OF STREAM FLOW DIVERSION

STEPHEN C. HART¹ AND ANGELA C. DiSALVO²

School of Forestry and Merriam-Powell Center for Environmental Research,
Northern Arizona University, Flagstaff, AZ 86011

White Mountain Research Station, University of California,
San Diego, La Jolla, CA 92093

ABSTRACT

We estimated aboveground and belowground net primary productivity (NPP) for two reaches of a montane riparian ecosystem in the eastern Sierra Nevada Mountains of California with differing stream flow regimes resulting from varying degrees of stream flow diversion for hydroelectric power generation. Total understory productivity (herbaceous and shrub) was 2.5 times higher ($P < 0.001$) at the high-flow site than at the low-flow site (22.4 and $8.9 \text{ g C m}^{-2} \text{ yr}^{-1}$, respectively). Annual litterfall was also higher ($P = 0.03$) at the high-flow ($235 \text{ g C m}^{-2} \text{ yr}^{-1}$) than at the low-flow site ($180 \text{ g C m}^{-2} \text{ yr}^{-1}$). However, tree and total aboveground NPP, as well as annual soil respiration and belowground NPP, were all statistically similar between sites. Furthermore, total (above- plus below-ground) NPP was statistically similar between sites (903 and $643 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the high- and low-flow sites, respectively). These productivity estimates are, to our knowledge, the first ever reported for a western montane riparian ecosystem. Our results suggest that NPP of montane riparian ecosystems located along gaining stream reaches is only loosely coupled to stream flow, and understory aboveground NPP may be the most sensitive productivity measure to altered stream flow.

Key Words: Net primary productivity, riparian ecosystems, Sierra Nevada Mountains, soil respiration, stream flow diversion.

Riparian ecosystems are among the most heavily disturbed ecosystems in the western United States (US) and have been reduced in area by over 80% since Euro-American settlement (Swift 1984). In the western US, riparian areas currently represent less than 1% of the landscape (Knopf et al. 1988). Although small in area relative to other ecosystem types, the value and influence of riparian areas are greatly disproportionate to their areal extent. For instance, of the 401 species of mammals, birds, reptiles, and amphibians in the Sierra Nevada Mountains of California, over 20% depend directly on riparian habitats, and many others use these areas for foraging, water, cover, shade, and travel corridors. Additionally, 24% of these riparian-dependent species are at risk of extinction (Garber 1996).

In the eastern Sierra Nevada Mountains, many montane riparian ecosystems have been influenced by small-scale hydroelectric facilities constructed primarily in the first quarter of the 20th Century; these hydroelectric plants diverted water away from natural stream channels to facilitate power generation (Harris et al. 1987; Kattelman 1996). The degree of stream flow diverted ranged from a few percent of the natural discharge to the complete de-

watering of the stream channel (Kattelman 1996). Typically, water is diverted throughout the entire year. The amount of spring runoff from rapidly melting snow is usually diminished and the timing delayed relative to the undiverted condition (due to water storage facilities associated with the hydroelectric plants), and sporadic releases of water below the diversion, corresponding to peak power demands, commonly occur (Kattelman 1996). About 20% of the total stream length in the Owens-Mono region has been completely diverted, while almost 90% has been impacted to some degree by diversion (Kondolf 1989). Water diversion reduces stream flow rates and can significantly alter the magnitude, frequency, duration, timing, and rate of change of hydrologic conditions (Poff et al. 1997). Changes in these important hydrologic characteristics can cause stress to riparian ecosystems, resulting in reduced growth (Reily and Johnson 1982), reduced recruitment, and increased mortality (Smith et al. 1991; Stromberg and Patten 1992; Rood et al. 1995). Responses of individual plant species to altered flow regimes will likely affect vegetation community structure (DiSalvo and Hart 2002), resulting potentially in loss of obligate riparian species, invasion by facultative riparian taxa, and reduction in the areal extent of the riparian corridor.

Previous studies have assessed the response of many structural and a few functional attributes of

¹ Author for correspondence, e-mail: steve.hart@nau.edu

² Present address: World Forestry Center, 4033 SW Canyon Road, Portland, OR 97221.

western riparian forests to altered stream flow from water diversion. These include: leaf area index, tree mortality, mature tree and juvenile density, radial growth variation, tree xylem water potential, tree leaf stomatal conductance, and water source utilization (Smith et al. 1991; Stromberg and Patten 1991, 1992). However, perhaps the most fundamental characteristic of an ecosystem is net primary productivity (NPP), given that all biological activity, including human activity, is dependent on this process (Whittaker 1975). Indeed, NPP of an ecosystem has been suggested as one of the key attributes for assessing the integrity ("health") of an ecosystem (Costanza 1992; Kolb et al. 1994), as well as the sustainability of management approaches (Christensen et al. 1996). Relatively few investigators have estimated total (i.e., above- and below-ground) NPP of forest ecosystems, and we know of no estimate of above or total net primary productivity for riparian forest ecosystems in the arid, western US.

We assessed the effects of stream flow diversion on the total NPP of a montane riparian ecosystem in the eastern Sierra Nevada Mountains of California. We believe that comparisons of NPP along reaches with different stream flow regimes will improve our understanding of the impacts of water manipulations on these rare and threatened, but vital ecosystems. Given the strong links between stream flow and tree radial growth observed previously in eastern Sierran riparian areas (Stromberg and Patten 1991, 1996; DiSalvo and Hart 2002), we hypothesized that NPP would be higher at sites with higher stream flows. Based on this hypothesis, we also predicted sites with higher stream flows would have concomitantly higher soil C and N pools and rates of soil respiration than sites with lower stream flows.

METHODS

Study Sites and Sampling Design

Our study was conducted on the east slope of the Sierra Nevada Mountains along Bishop Creek, Inyo County, California (Fig. 1). Bishop Creek drains a 180-km² watershed in the rain shadow of the Sierra Nevada Mountains. Mean annual precipitation ranges from about 100 cm (primarily as winter snow) at the upper end of the watershed (ca. 4500 m elevation) to about 15 cm (primarily as winter rain) at the confluence of Bishop Creek with the Owens Valley River (ca. 1350 m elevation). Bishop Creek flows over bedrock and glacial till in its upper reaches, through a steep, glacially carved canyon surrounded by alpine and coniferous forest vegetation. In its mid and lower reaches, the creek is surrounded by Great Basin shrub desert and dissects an alluvial fan before entering the Owens River Valley (Stromberg and Patten 1992). Bishop Creek has a well-defined series of stream flow diversions, which includes three catchment lakes, two

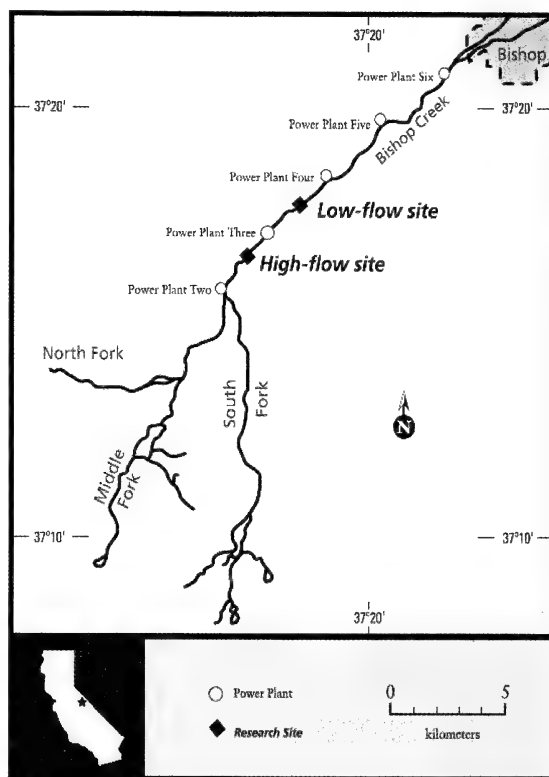


FIG. 1. Location of high- and low-flow sites along Bishop Creek, California. The black squares denote the approximate locations of the two plots assessed at each site. Modified from DiSalvo and Hart (2002).

primary intakes, and five power stations. Stream flows within this watershed have been diverted for nearly a century (Stromberg and Patten 1991), and little information is available on pre-diversion conditions.

Hydrogeomorphological and physiographic factors differ among stream reaches in the mountainous arid western U.S. (Jones and Stokes Associates 1985; Kondolf et al. 1987), and many of the creeks draining the eastern Sierra Nevada Mountains have diverted stream flows (Stromberg and Patten 1992). Hence, we compared riparian ecosystems within the Bishop Creek Watershed along reaches of Bishop Creek with varying degrees of water diversion.

A "high-flow" site (37°17'45"N, 118°32'30"W) and a "low-flow" site (37°18'15"N, 118°31'15"W) were selected for study based on the magnitude of minimum stream flows maintained by Southern California Edison (SCE) within Bishop Creek, as required by the Federal Energy and Regulatory Commission (FERC 1994). Both sites were located along gaining (ground water to stream water) reaches (Space et al. 1989). These two sites were separated by Power Plant 3, and included riparian vegetation growing in a streamside environment. Sites were similar in elevation (1980 and 1910 m

for the high- and low-flow sites, respectively), and were within 1.5 km of each other (Fig. 1). Great Basin shrub desert characterized the upland vegetation at both sites (Chambers Group 1994). Soils at these sites have very low plant-available water storage capacities (Chambers Group 1994) and are members of the Typic Xerorthent, sandy-skeletal, mixed, frigid Soil Taxonomic family (USDA Forest Service 1995). Sites were located within narrow glacial valleys, with an average channel gradient of 11% for the high-flow site and 13% for the low-flow site (Chambers Group 1994). The sites had similar overstories dominated by: *Pinus jeffreyi* Grev. & Balf. (Pinaceae), *Betula occidentalis* Hook. (Betulaceae), *Populus trichocarpa* Torr. & Gray (Salicaceae), and to a lesser extent *Salix* spp. (primarily *S. lasiolepis* Benth. [Salicaceae]). *Pinus jeffreyi*, although not typically considered a “riparian species,” is a common member of montane riparian communities of the eastern Sierra, and its occurrence is limited to these environments at lower elevations within these watersheds (Stromberg and Patten 1990; S. C. Hart personal observation). *Pinus monophylla* Torr. & Frém. (Pinaceae) was found at the drier, more upland edges of the riparian corridors. Understories were dominated by *Rosa woodsii* Lindl. var. *ultramontana* (S. Wats.) Jepson (Rosaceae), but also present were *Artemisia tridentata* Rydb. (Asteraceae), *Chrysothamnus nauseosus* Pallas (Asteraceae), and *Purshia tridentata* Pursh (Rosaceae).

Two 50-m long plots were established at each site parallel to the stream, with plot widths extending on both sides of the stream (the stream itself was generally <5 m wide). Plots at each site were not contiguous (separated by at least 50 m), and their location was determined at random with the constraint of matching hydrogeomorphological and physiographic factors of the high-and low-flow sites as closely as possible. The high-flow site was located far enough upstream so that it was not influenced by water impoundment immediately above Power Plant 3. Plot width was determined by the extent of the canopy of obligate riparian vegetation (i.e., *Betula*, *Populus*, and *Salix*) on each side of the stream (Mueller-Dombois and Ellenberg 1974), and thus plot size varied depending upon riparian corridor width (ranging from 20 to 40 m). Plot area (1620–1940 m²) was determined using Trimble GPS units and Pathfinder Office (Pathfinder Office, version 2.0, Trimble, Sunnyvale, CA). The accuracy of these differentially corrected measurements is estimated to be about one meter.

A set of nested subplots (~1 m²) was used for taking soil and litterfall measurements and for sampling adequately all vegetation types within the riparian zone (Bonham 1989). Within each plot, two transects were established, one on each side of the stream and approximately parallel and midway between the stream channel and the edge of the riparian corridor. Subplots were located randomly ei-

ther 5 m towards or away from the stream at 10-m intervals along each transect (n = 10/plot). In these subplots, we measured soil respiration, soil water content, and litterfall (see below). Understory vegetation was sampled within three 0.32 m × 1.25 m quadrats placed side by side and offset 5-m downstream from soil and litterfall subplots (n = 10/plot). Shrubs were sampled within all three quadrats (total area per subplot = 1.2 m²), while herbaceous species were sampled within one of the three quadrats chosen at random (total area per subplot = 0.4 m²).

Microclimatic, Soil, and Stream Measurements

Campbell Scientific (Campbell Scientific Inc., Logan, UT) CR10 dataloggers were used to record microclimatic measurements from 26 May 1999 to 25 May 2000. One datalogger was placed at the upstream plot of the high-flow site and another was placed at the downstream plot of the low-flow site. Dataloggers were located midway between the stream edge and the edge of the riparian corridor. Daily mean soil temperatures were measured using thermistors placed at a 7.5-cm mineral soil depth in environments representative of the plot (n = 4/site). Mean daily air temperature and relative humidity were measured using Vaisala 50Y Temperature and RH probes (Vaisala, Inc., Woburn, MA). Total daily precipitation was measured using an unheated tipping bucket rain gauge placed in an open area outside the riparian corridor (model TE525, Texas Electronics, Inc., Dallas, TX).

Soil volumetric water content was measured approximately monthly from May through November 1999 with a Trace Systems (Soil Moisture Corp., Santa Barbara, CA) time domain reflectometry unit and probes of 0–15, 0–30, and 0–60 cm in length placed adjacent to soil respiration measurements (n = 10 per plot for 0–15 cm and 15–30 cm depths; n = 5 per plot for 30–60 cm depth). Volumetric water contents of the 15–30 and 30–60 cm depths were calculated from the volumetric contents of the 0–15, 0–30, and 0–60 cm probe sets (Kolb et al. 1997).

In May 2000, forest floor (O horizon) mass per unit area (areal density) was estimated for each plot using a 0.093-m² quadrat placed at five of the ten subplots selected at random. Organic matter greater than one centimeter in diameter was discarded, and the remaining material was oven-dried at 70°C. Below the O horizon samples, 5-cm diameter mineral soil cores were removed to a 15-cm depth. Soil samples were air-dried, sieved (=2 mm), ground to a fine powder on a bar mill, and then analyzed for total carbon (C) and nitrogen (N) on an elemental analyzer (Model NC2100, CE Elantech, Inc., Lakewood, NJ). Total soil C and N concentrations were then converted to an oven-dry (105°C) basis using the gravimetric water contents of air-dried soils determined from soil subsamples.

Mean daily stream flow values were obtained from SCE for diversion points directly above our study sites. As part of a riparian monitoring program, SCE has installed gaging stations to determine flows released from power plant locations along Bishop Creek. Read (1994) compared in-stream flow measurements to upstream gaging station stream flows and found that the two measurements were similar and highly correlated.

Aboveground Net Primary Productivity and Leaf Area

Aboveground net primary productivity (ANPP) was estimated as the sum of increases in aboveground standing crop of vegetation plus litterfall (Grier et al. 1989). Biomass losses due to herbivory were not measured; recent studies across a wide range of terrestrial ecosystems suggest that herbivores consume approximately 10 to 20% of ANPP in any given, non-outbreak year (Cyr and Pace 1993; Cebrian 1999). No domestic animal grazing occurred at these sites.

Aboveground herbaceous productivity was assumed to be equivalent to the peak standing crop of the aboveground biomass (Bonham 1989). All aboveground herbaceous biomass was harvested in mid-September, 1999, oven-dried at 70°C, and weighed. Aboveground shrub productivity (stems plus leaves) was estimated at the same time by harvesting and drying current-year growth (Bonham 1989; Grier et al. 1989). Current growth of shrubs was distinguished by differences in color between the current year's and previous year's growth. This approach was verified by marking several stems of each species before the 1999 growing season (Bonham 1989).

Tree productivity was determined for all stems over five cm in diameter at breast height (DBH, 1.4 m) within each plot. We assumed that the contribution from trees with stems < 5 cm DBH to ANPP was relatively small (Whittaker et al. 1974). Stem diameter measurements and increment cores were taken at the end of the 1999 growing season. These data were used in allometric equations found in the literature for each species or a related species to predict aboveground tree biomass in 1998 and 1999. Two increment cores perpendicular to each other were taken at breast height from each tree stem within a plot (a subsample of stems were used with *B. occidentalis*; see below). Increment cores were mounted and sanded following standard methods (Phipps 1985). The 1999 stem radial increment of each core was measured to the nearest 0.001 mm under 20× magnification using an automated measurement system. Radial increments determined on the two cores per stem were averaged and then used to determine the DBH of the stem in 1998 and 1999.

Allometric equations for *P. trichocarpa* and *Salix* spp. were taken from BIOPAK (Means et al. 1994)

and the *P. monophylla* equation from Miller et al. (1981). For *P. jeffreyi*, the equations found in the literature (Means et al. 1994) estimated only tree bole biomass. An allometric equation for bole biomass of *Pinus ponderosa* Dougl. ex Laws. (Pinaceae), developed using data from Gholz et al. (1982) and W. W. Covington (Northern Arizona University, unpublished data), produced nearly identical tree bole biomass values as the equation for *P. jeffreyi* across the range in tree diameters at our sites (two-tailed t-test, $P = 0.35$); additionally, bole biomass estimates were highly correlated ($r^2 = 0.998$, $P < 0.001$), although the *P. ponderosa* equations slightly underestimated *P. jeffreyi* bole biomass (slope = 1.07). Hence, we assumed that the allometries among the other tree components would also be similar between the two species and estimated aboveground tree biomass of *P. jeffreyi* by adding tree bole biomass determined using the equation for *P. jeffreyi* (Means et al. 1994) to foliage and branch biomasses calculated using the equations for *P. ponderosa* (Kaye et al. in press).

No suitable equation was found for *B. occidentalis*, so we developed our own equation based upon stem basal diameter (DBA) using stems ranging in size from 4.6 to 11 cm DBA located adjacent to our plots (total foliar biomass = $\exp(\ln(\text{DBA}) \times 1.591 + 2.861)$, $n = 5$, $P = 0.04$, $r^2 = 0.81$; total stem biomass = $\exp(\ln(\text{DBA}) \times 2.090 + 4.765)$, $n = 5$, $P < 0.01$, $r^2 = 0.97$; DBA in cm, biomass in g). Due to the large number of stems per plot (mean of 592 stems ha^{-1}), a random subsample (approximately 20%) of *B. occidentalis* stems was selected for increment core analysis. A relationship between basal area increment (BAI) per tree and DBA was then derived to estimate tree growth for the 1999 growing season for individuals not measured directly ($n = 72$, $P < 0.01$, $r^2 = 0.11$). Although this relationship is weak, it was the best predictor of productivity from *B. occidentalis*, which comprised only 0 to 3% of the total stem productivity among the plots. *B. occidentalis* stems grow in clumps and other factors (number of stems in clump, stem age) may impact the relationship between BAI and DBA; however, including stem number per tree in the regression equation did not significantly improve its predictive power (data not shown).

Litterfall was collected approximately monthly from 26 May 1999 through 25 May 2000 using circular 0.066 m^2 littertraps (Grier et al. 1989). Littertraps were located within the same subplots where soil measurements were taken, as well as five additional locations in each plot determined at random. Collected litter was sorted by species and plant component (i.e., foliage, flower, wood), oven dried at 70°C, and weighed. Aboveground net primary productivity of trees was calculated by summing the changes in aboveground biomass of tree components between 1998 and 1999 and litterfall estimated over the 1999–2000 period. Biomass and productivity values were converted to a C basis as-

suming that dry biomass was 50% C (Runyon et al. 1994).

We measured leaf area index (LAI) because it frequently correlates with NPP in many forest types (Perry 1994), and previous researchers have found it to be a sensitive measure of structural changes that result from stream flow reduction in western riparian ecosystems (Stromberg and Patten 1996). Projected LAI values were determined by species for each plot using mean specific leaf areas (area per unit mass) measured on these same plots (K. Alstad, Northern Arizona University, unpublished data) and litterfall mass collected in littertraps. Litterfall masses were corrected for reabsorption prior to leaf abscission assuming a 15% loss of mass for *P. jeffreyi* and *P. monophylla* and a 20% loss of mass for the deciduous trees (i.e., *B. occidentalis*, *P. trichocarpa*, and *Salix* spp.; Sedell et al. 1974). *Pinus jeffreyi* and *P. monophylla* LAI values were also adjusted assuming a leaf turnover rate of 0.25/yr (Running 1994).

Soil Respiration and Belowground Productivity

We measured soil respiration monthly from May through November 1999 using a LI-COR 6200 portable photosynthesis system (LI-COR Inc., Lincoln, NE) equipped with an 11.9-l chamber (27.5 cm diameter, 20 cm height; Kaye and Hart 1998). The gas exchange system was calibrated in the field prior to CO₂ flux measurements. Carbon dioxide concentrations were measured over a three-minute period. Carbon dioxide flux was calculated from the linear change in CO₂ concentration in the chamber with time using least squares regression. Ambient air temperature and soil temperature were measured at the time of the respiration measurement. Soil temperature was recorded at a 7.5-cm mineral soil depth or 7.5-cm depth below the ground surface if no mineral horizon was present (i.e., an organic soil profile). Soil respiration measurements were taken within each plot during the same time interval (10:00–14:00 h) on consecutive days; the order by which plots were measured was assigned at random each month. Every month on 10 different subplots, soil respiration measurements were taken every 6 h over a 24-h period to assess diel variation. However, analysis of variance indicated that time of day was not a significant factor in any month or plot ($P > 0.68$; data not shown). Hence, soil respiration measurements taken at a set point during the day were assumed to be representative of the daily flux, and CO₂ fluxes ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) for each subplot were scaled to daily values by multiplying these fluxes by the number of seconds in a 24 h period. Total growing season respiration was determined by integrating daily respiration rates over the growing season (Kaye and Hart 1998).

Soil respiration was not measured during “winter” months (1 January 1999 to mid-April, and in December 1999). Various winter respiration models

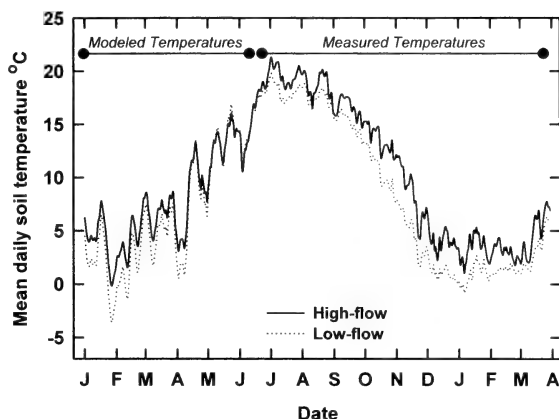


FIG. 2. Mean daily soil temperatures (7.5 cm depth) at the high- and low-flow sites during 1999. Values between May 26 and December 31 were measured using dataloggers and thermistors placed at locations representative of microenvironments at each site ($n = 4/\text{site}$). Values between January 1 and May 25 were modeled using mean daily air temperatures recorded at Bishop, California. The high-flow site had significantly higher soil temperatures ($P < 0.01$, RM ANOVA on ranks).

were tested using combinations of soil volumetric water content, air temperature, and soil temperature under environmental conditions likely reflective of the winter period (i.e., soil temperatures below 16°C and soil volumetric water content [0–15 cm] above 0.06 m³/m³; Figs. 2 and 3). The model that gave the best fit between soil respiration and these environmental conditions was: soil respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) = $\exp [-0.358 + (0.303 \times ^\circ\text{C}) - (0.0121 \times ^\circ\text{C}^2)]$, where $r^2 = 0.437$, $P = 0.002$, and $n = 33$. Soil temperatures were not measured for the entire winter period, so we developed equations that estimated soil temperatures at our sites from air temperatures measured at Bishop, California ($r^2 = 0.92$ to 0.93 , $P < 0.001$). Annual soil respiration was calculated as the sum of measured growing season respiration and modeled winter respiration.

We estimated belowground net primary productivity (BNPP) in our plots from belowground C allocation (BCA) measurements (Raich and Nadelhoffer 1989). Assuming annual changes in soil C pools are small in magnitude relative to loss of C via soil respiration and inputs of C from litterfall (Giardina and Ryan 2002), BCA can be estimated from the equation: $\text{BCA} = \text{soil respired C} - \text{litterfall C}$. Belowground net primary productivity was determined by assuming that root productivity is one-half of BCA and biomass is 50% C (Runyon et al. 1994). Vogt et al. (1998) provides a detailed discussion of the advantages and disadvantages of different methods for estimating BNPP at the ecosystem scale.

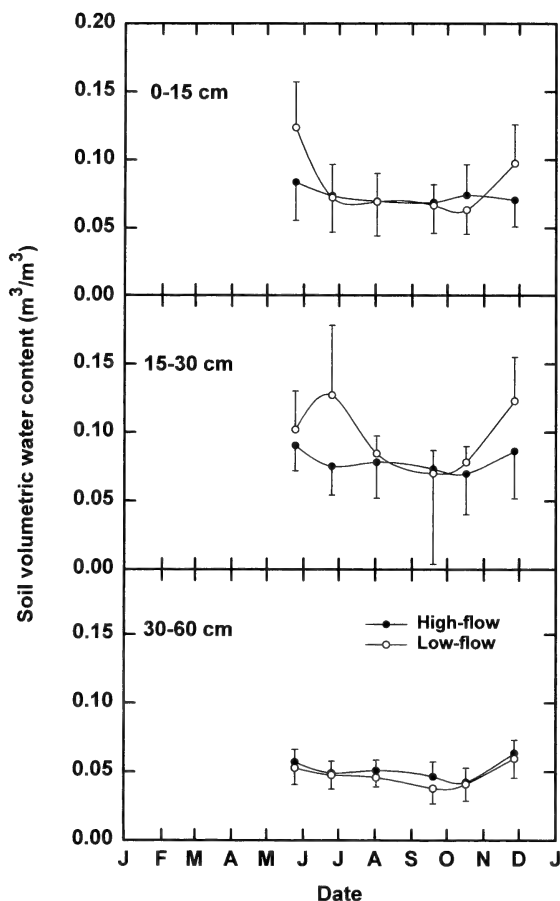


FIG. 3. Mean soil volumetric water content at different soil depths at the high- and low-flow sites during 1999. Vertical bars denote one standard error of the mean ($n = 2$). Error bars for each mean value are shown only in one direction in order to improve clarity. No significant difference in soil volumetric water content was found between sites at any soil depth ($P > 0.05$, RM ANOVA).

Statistical Analyses

Two-tailed t-tests were used to evaluate differences in forest floor mass, mineral soil C and N concentrations, standing biomass, and productivity measures between sites. Repeated measures analyses of variance (RM ANOVA) were used to assess site differences in soil volumetric water content and soil respiration. Repeated measures analyses of variance on ranks were used to test for differences in air and soil temperature, relative humidity, and stream flow between sites because these data violated one of the assumptions of parametric ANOVA.

All analyses were performed with StatView (version 4.5, Abacus Concepts, Inc., Berkeley, CA) except for RM ANOVA on ranks tests, which were performed using SigmaStat (version 2.0, Systat Software, Inc., Richmond, CA). The $P \leq 0.05$ level was used to denote statistical significance.

RESULTS

Median air and soil temperatures were significantly higher at the high-flow than at the low-flow site, but these differences were small in magnitude ($\leq 1.3^\circ\text{C}$; Table 1, Fig. 2). Median relative humidity was lower at the high-flow than the low-flow site, but the magnitude of difference was also relatively minor (3.7%; Table 1). Annual precipitation was 110 mm and 136 mm at the high- and low-flow sites, respectively (Table 1); however, over 90% of this difference occurred during the non-growing season months (data not shown). Annual precipitation at our study sites over the past 74 years, estimated from a correlation between monthly precipitation values measured at our sites and the Bishop Airport, CA (1260 m elevation, <20 km away; $r^2 = 0.81$, $P < 0.001$, $n = 12$), ranged from 71 to 595 mm (mean of 236 mm and CV of 46%).

No significant differences were found in volumetric water content at any depth between sites (Fig. 3). Volumetric soil water content was low ($<14\%$) in all soil depths in these skeletal, coarse-

TABLE 1. SELECTED SITE CHARACTERISTICS OF RIPARIAN SITES ALONG BISHOP CREEK, CALIFORNIA. ^a Data shown are modeled values for 1 January 1999 to 25 May 1999 and measured values for 26 May 1999 to 31 December 1999 (see text). ^b Precipitation values are for 26 May 1999 to 25 May 2000; annual precipitation was not tested for difference between sites due to lack of replication. ^c Probability values for tests of differences between sites using RM ANOVA on ranks for air and soil temperatures and relative humidity; parametric RM ANOVAs were used for forest floor mass and soil carbon (C) and nitrogen (N) concentrations.

| Characteristic | Site | | P value ^c |
|---|-----------|----------|----------------------|
| | High-flow | Low-flow | |
| Median daily air temperature ($^\circ\text{C}$) ^a | 16.5 | 15.2 | <0.001 |
| Median daily soil temperature ($^\circ\text{C}$) ^a | 15.3 | 14.4 | <0.001 |
| Median daily relative humidity (%) ^a | 25.5 | 29.2 | <0.001 |
| Annual precipitation (mm) ^b | 136 | 110 | — |
| Mean forest floor mass (g/m^2) | 25.6 | 17.4 | 0.21 |
| Mean soil C concentration ($\text{g C}/\text{kg}$) | 21.8 | 26.5 | 0.71 |
| Mean soil N concentration ($\text{g N}/\text{kg}$) | 0.88 | 1.1 | 0.69 |

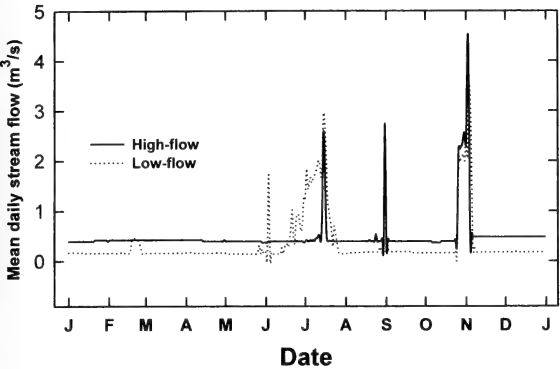


FIG. 4. Mean daily stream flow at high- and low-flow sites during 1999. Daily stream flow at the high-flow site was significantly higher than stream flow at the low-flow site ($P < 0.001$, RM ANOVA on ranks).

textured soils. No significant differences existed between sites for forest floor mass, mineral soil C concentration, or mineral soil N concentration (Table 1).

Median daily stream flow (discharge) for the high-flow site for 1999 was $0.39 \text{ m}^3/\text{s}$ and was significantly higher than the low-flow site stream flow of $0.17 \text{ m}^3/\text{s}$ (Fig. 4). Annual stream flow over this period was $16 \times 10^6 \text{ m}^3$ and $11 \times 10^6 \text{ m}^3$ at the high- and low-flow sites, respectively. Median daily stream flow during the growing season (May–Oct.) was significantly higher at the high-flow site ($0.40 \text{ m}^3/\text{s}$) than at the low-flow site ($0.17 \text{ m}^3/\text{s}$; Fig. 4). Total growing season stream flow was $8.1 \times 10^6 \text{ m}^3$ and $7.5 \times 10^6 \text{ m}^3$ at the high- and low-flow sites, respectively. However, most of these differences in stream flow between sites occurred because of differences in base flows rather than peak flows (Fig. 4).

Mean ANPP of herbs was $7.5 \text{ g C m}^2 \text{ yr}^{-1}$ at the high-flow site and $3.6 \text{ g C m}^2 \text{ yr}^{-1}$ at the low-flow site, but these differences were not statistically significant ($P = 0.623$). Mean ANPP of shrubs was $14.9 \text{ g C m}^2 \text{ yr}^{-1}$ at the high-flow site and $5.4 \text{ g C m}^2 \text{ yr}^{-1}$ at the low-flow site, but these values also were similar statistically ($P = 0.288$). Shrub productivity at both sites was dominated by *Rosa woodsii* var. *ultramontana*, however, this species contributed less to shrub ANPP at the high-flow site (69%) than at the low-flow site (88%) site. Above-ground NPP of the second most prevalent shrub species, *Artemesia tridentata*, represented approximately 10% of total shrub production at both sites and was not statistically different between sites. However, total understory (herbaceous and shrub combined) ANPP was 2.5 times greater at the high-flow site ($22.4 \text{ g C m}^2 \text{ yr}^{-1}$) than at the low-flow site ($8.9 \text{ g C m}^2 \text{ yr}^{-1}$), and this difference was highly significant (Table 2).

Mean aboveground tree biomass at the beginning of 1999 was similar statistically at the high-flow

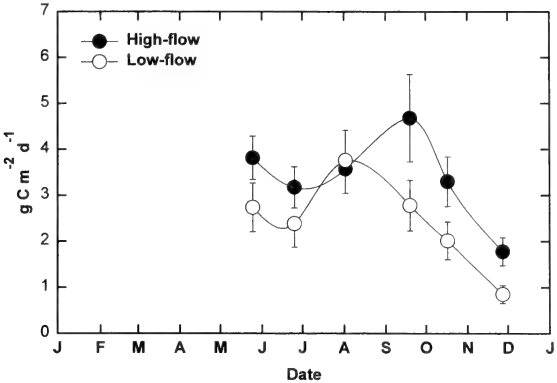


FIG. 5. Mean daily soil respiration from high- and low-flow sites during 1999. Vertical bars denote ± 1 standard error of the mean ($n = 2$). Soil respiration rates were statistically similar between sites ($P = 0.09$, RM ANOVA).

site (11.6 kg C/m^2) and the low-flow site (7.25 kg C/m^2 ; Table 2). The majority of aboveground tree biomass was contributed by the species *Pinus jeffreyi*, which represented 94% and 87% of the total tree biomass in the high- and the low-flow sites, respectively. No significant differences in above-ground tree biomass were found between sites for any individual tree species with the exception of *Populus trichocarpa*, which had significantly higher aboveground biomass at the low-flow site (Table 2). The annual change in aboveground tree biomass (ΔB) between 1998 and 1999 was also dominated by *P. jeffreyi* at both sites, where growth of this species comprised 80 to 85% of total ΔB ; however, both total ΔB and ΔB of *P. jeffreyi* alone were similar statistically between sites (Table 2). The only statistically significant differences in ΔB between sites for individual tree species occurred for *Pinus monophylla* and *P. trichocarpa*, where ΔB was higher at the low-flow site (Table 2).

Annual litterfall at the high-flow site was 235 g C/m^2 , which was significantly greater than at the low-flow site (180 g C/m^2 ; Table 2). *Pinus jeffreyi* contributed the most litterfall at both sites (51% and 44% of the total for high- and low-flow sites, respectively), and litterfall from this species was significantly higher at the high-flow than at the low-flow site. No other tree species had significantly different litterfall between sites (Table 2). Wood, shrub, and unidentifiable material contributed approximately 17%, 3%, and 1%, respectively, to the total annual litterfall at both sites (Table 2; not all data shown). Leaf area comparisons between sites and among tree species generally followed a similar pattern as annual litterfall (Table 2).

Mean tree ANPP ($\Delta B + \text{litterfall}$) was statistically similar between sites for all individual species and for total tree ANPP (Table 2; total tree ANPP not shown). Furthermore, mean total ANPP (sum of herbaceous, shrub, and tree ANPP) was statisti-

TABLE 2. LEAF AREA, ABOVEGROUND BIOMASS, AND COMPONENTS OF NET PRIMARY PRODUCTIVITY AT HIGH- AND LOW-FLOW SITES ALONG BISHOP CREEK, CA. ^a Means \pm 1 SE; n = 2. ^b Probability values for a significant difference in that component between sites (two-tailed t-tests).

| Component | Site | | P value ^b |
|--|---------------|-------------|----------------------|
| | High-flow | Low-flow | |
| 1998 Projected Leaf Area Index (m ² /m ²) | | | |
| <i>P. jeffreyi</i> | 1.8 ± 0.2 | 1.1 ± 0.1 | 0.06 |
| <i>P. monophylla</i> | 0.17 ± 0.16 | 0.12 ± 0.07 | 0.80 |
| <i>P. trichocarpa</i> | 1.6 ± 1.3 | 3.1 ± 0.4 | 0.40 |
| <i>B. occidentalis</i> | 1.0 ± 0.4 | 1.1 ± 0.1 | 0.82 |
| <i>Salix</i> spp. | 0.11 ± 0.03 | 0.02 ± 0.00 | 0.06 |
| Total | 4.7 ± 1.0 | 5.4 ± 0.2 | 0.52 |
| 1998 aboveground tree biomass (g C/m ²) | | | |
| <i>P. jeffreyi</i> | 10,940 ± 1420 | 6308 ± 781 | 0.10 |
| <i>P. monophylla</i> | 59.5 ± 38.4 | 353 ± 120 | 0.15 |
| <i>P. trichocarpa</i> | 193 ± 7 | 309 ± 22 | 0.04 |
| <i>B. occidentalis</i> | 453 ± 156 | 230 ± 89 | 0.34 |
| <i>Salix</i> spp. | 0.0 | 54.2 ± 51.0 | 0.40 |
| Total | 11,640 ± 1230 | 7254 ± 917 | 0.10 |
| Change in tree biomass 1998–1999 (g C/m ²) | | | |
| <i>P. jeffreyi</i> | 193 ± 57 | 127 ± 37 | 0.44 |
| <i>P. monophylla</i> | 1.2 ± 0.3 | 4.2 ± 0.6 | 0.04 |
| <i>P. trichocarpa</i> | 8.2 ± 0.3 | 10.1 ± 0.2 | 0.03 |
| <i>B. occidentalis</i> | 26.2 ± 6.8 | 12.1 ± 4.0 | 0.22 |
| <i>Salix</i> spp. | 0.0 | 1.7 ± 1.7 | 0.41 |
| Total | 228 ± 50 | 155 ± 40 | 0.38 |
| Leaf litter production (g C m ⁻² yr ⁻¹) | | | |
| <i>P. jeffreyi</i> | 122 ± 9 | 53.4 ± 2.3 | 0.02 |
| <i>P. monophylla</i> | 4.8 ± 4.6 | 3.3 ± 2.0 | 0.79 |
| <i>P. trichocarpa</i> | 37.9 ± 30.3 | 61.0 ± 7.4 | 0.53 |
| <i>B. occidentalis</i> | 26.1 ± 8.0 | 32.5 ± 3.2 | 0.53 |
| <i>Salix</i> spp. | 4.5 ± 1.0 | 0.8 ± 0.1 | 0.07 |
| Total tree leaf litter production | 195 ± 19 | 151 ± 5 | 0.15 |
| Total litter production | 235 ± 0.3 | 180 ± 9 | 0.03 |
| Total aboveground NPP (g C m ⁻² yr ⁻¹) | | | |
| <i>P. jeffreyi</i> | 314 ± 66 | 181 ± 35 | 0.21 |
| <i>P. monophylla</i> | 6.0 ± 4.9 | 7.5 ± 2.5 | 0.81 |
| <i>P. trichocarpa</i> | 46.0 ± 30.6 | 71.1 ± 7.2 | 0.51 |
| <i>B. occidentalis</i> | 52.3 ± 1.2 | 44.6 ± 7.2 | 0.40 |
| <i>Salix</i> spp. | 4.5 ± 1.0 | 2.5 ± 1.7 | 0.42 |
| Herbaceous and shrub | 22.4 ± 0.2 | 8.9 ± 0.5 | 0.002 |
| Total aboveground | 468 ± 30 | 324 ± 37 | 0.09 |
| Soil respiration (g C m ⁻² yr ⁻¹) | 1126 ± 213 | 828 ± 59 | 0.31 |
| Belowground NPP (g C m ⁻² yr ⁻¹) | 434 ± 107 | 319 ± 25 | 0.40 |
| Total ecosystem NPP (g C m ⁻² yr ⁻¹) | 903 ± 137 | 643 ± 11 | 0.20 |

cally similar between the high-flow site (468 g C m⁻² yr⁻¹) and the low-flow site (324 g C m⁻² yr⁻¹; Table 2).

Mean soil respiration rates measured between May and November 1999 were similar statistically between the high- and low-flow sites; however, soil respiration rates were consistently higher at the high-flow site, except for the August sampling period when stream flow was actually higher at the low-flow site (Fig. 4). Annual soil respiration was estimated as 1126 and 828 g C/m² in the high- and low-flow sites, respectively, and did not differ between sites (Table 2). Mean BNPP values calculated from C balance were statistically similar be-

tween sites (434 and 319 g C m⁻² yr⁻¹ for the high- and low-flow sites, respectively; Table 2). Mean total NPP (ANPP plus BNPP) of the entire ecosystem was also statistically similar between the high-flow site (903 g C m⁻² yr⁻¹) and the low-flow site (643 g C m⁻² yr⁻¹; Table 2). The ratio of BNPP to total NPP was close to 0.5 at both sites (Table 2).

DISCUSSION

Tree growth has been shown to be tightly coupled to stream flow in some riparian forests of the western U.S. (Stromberg and Patten 1990, 1991, 1992, 1996; DiSalvo and Hart 2002; Galuszka and

Kolb 2002). Stream, soil, and ground water may all serve as sources of water for trees in these ecosystems depending on the relative availability of the source and the rooting habit of the tree species (Smith et al. 1991). Reservoirs and diversions that alter stream flow reduce high flow periods (i.e., spring snow melt) that recharge aquifers and soils. Over the life-span of the riparian vegetation, stream flow reduction via diversion could reduce NPP by decreasing water availability to plants within the riparian corridor. Over the longer term, stream flow reductions caused by water diversion could reduce NPP by altering plant community composition, reducing leaf area index, or both.

Contrary to our hypothesis, most of the productivity measures we assessed (i.e., change in above-ground tree biomass, total ANPP, BNPP, and total NPP) were not higher at the site with higher stream flows in 1999. However, annual litterfall (due to higher litter production by *Pinus jeffreyi*) and understory (herbaceous plus shrub) ANPP were significantly higher at the high-flow site. We speculate that a shallower rooting distribution of the understory compared to the overstory trees contributed to the lower ANPP of the understory at the riparian site with a lower stream flow.

If this is indeed the mechanism responsible for the difference in understory productivity between the sites, then we would have expected to find a difference in the availability of water in surface soils at the two sites. However, our monthly measurements of soil water content showed no significant differences between the high-flow and the low-flow sites at any soil depth. Monthly measurements of soil water content, particularly near the surface, may be insufficient for documenting soil water dynamics in the coarse-textured, skeletal soils of these riparian sites because of their low capacity to store water (USDA Forest Service 1995); low water storage capacity should lead to relatively rapid changes in soil water content in response to changes in stream flow and ground water depth (Brady and Weil 2001). Other possible mechanisms that may account for the observed differences in understory ANPP between sites include depth to ground water, soil nutrient availability, solar irradiance, and temperature.

Unfortunately, we were unable to directly measure ground water depth due to the prohibitive cost of drilling wells in the rocky soils found at our sites. However, Read (1994) examined ground water depth from 1991–1993 along a gaining and a losing reach of Bishop Creek within a few kilometers of our sites. She found that average depth to ground water was approximately 0.7 to 1.2 m despite variation in stream flows from less than 0.14 m³/s to more than 1.70 m³/s. Hence, it is unlikely that there were any large differences in depth to ground water between the two sites. Although we did not assess nutrient availability directly, the similar total C and N pools in soils at these sites

do not support differences in nutrient availability as a possible mechanism. Furthermore, we measured total irradiance at the meteorological stations installed at each site and found no significant difference (data not shown). Hence, it is unlikely that differences in photosynthetically active radiation contributed to the patterns we observed. Air and soil temperatures were slightly higher at the high-flow site, and tree growth is weakly correlated to maximum air temperature at these sites (DiSalvo and Hart 2002). Hence, higher temperatures and a longer growing season (Fig. 2) could have also contributed to the differences in understory ANPP between sites that we observed.

Stream flows during the growing season may better represent the relationship between water supply and the NPP of riparian ecosystems than total annual flows. Stromberg and Patten (1991) found that growing-season stream flow correlated better with annual tree-ring growth of *Populus* spp. than did annual stream flow within the Bishop Creek Watershed. Although 1999 annual stream flow at the high-flow site was 30% higher than at the low-flow site, stream flow during the 1999 growing season was only 8% higher. Furthermore, growing-season stream flows in 1999 at both these sites were higher than the average flows estimated between 1969 and 1988 (ca. 8.6×10^6 m³/yr; Stromberg and Patten 1991). If stream flow is a significant factor controlling NPP in these ecosystems, we would expect much larger differences in NPP between our sites during low-flow years when the disparity between sites in growing season stream flows would likely be magnified.

Differences in stream flow between the two sites were due primarily to higher base flows at the high-flow site. It is unclear in these montane riparian ecosystems if higher peak flows or higher base flows are more important in regulating NPP. Higher peak flows may result in greater recharge of soil water farther away from the active stream channel, but higher base flows likely provide higher sustained soil water availability near the stream channel. We speculate that higher base flows are likely more important within the upper reaches of the Bishop Creek Watershed because of the relatively narrow riparian corridors and low soil water storage capacities. Future studies need to experimentally determine how differences in stream flow characteristics alter NPP in these and other riparian ecosystems with regulated stream flows, particularly given these two characteristics are largely under the control of water managers.

Because this was an observational study that was also unreplicated at the “treatment” (i.e., stream diversion) level, we cannot unambiguously attribute any differences between sites to stream flow diversion. The vast majority of the trees at both these sites were established post-diversion (DiSalvo unpublished data); hence, current stand structural differences observed between sites (Table 2) are prob-

ably the cumulative result of decades of altered stream flows. Although ANPP of *P. jeffreyi* was not significantly higher at the high-flow site, litter production (which often is a good index of ANPP; Perry 1994) was higher. Hence, we speculate that the lack of a significant difference in ANPP between sites is a combined result of a small seasonal difference in stream flows between these sites in 1999, as well as lack of statistical power in our experimental design (see below). Indeed, previous research at these and similar sites have shown that radial growth of many of the tree species (including *P. jeffreyi*) is correlated to stream flow across years (Stromberg and Patten 1990, 1991, 1996; DiSalvo and Hart 2002); like litterfall, radial growth should be positively correlated to ANPP (Perry 1994).

We used estimated changes in standing aboveground biomass of *P. jeffreyi* between the high- and low-flow sites during the decade of the 1990s to evaluate this hypothesis. Differences in growing season stream flows between sites during this period on average were much greater than in 1999 (DiSalvo and Hart 2002; DiSalvo, unpublished data). This retrospective analysis was possible because we measured diameter increment over the previous decade in this species, and the allometric equations used to predict biomass required only DBH (DiSalvo and Hart 2002). We found that changes in aboveground standing biomass (ΔB) averaged 29% higher at the high-flow site than at the low-flow site over this decade (RM ANOVA, $P < 0.001$). Because *P. jeffreyi* contributed the vast majority of the ANPP at both sites in 1999 (Table 2), this result suggests that ANPP also was higher in the high-flow site over this period. We stress the need for replicated experimental manipulations of stream flow in riparian ecosystems for establishing unequivocally the relationship between stream flow diversion and NPP in these and other riparian ecosystems.

To our knowledge, the estimates of NPP given in this paper are the first ever reported for a western montane riparian ecosystem, and we know of only one other study (Clawson et al. 2001) that has previously estimated the belowground NPP of any riparian ecosystem worldwide. Aboveground productivity values (ranging between 288 and 499 g C m⁻² yr⁻¹ among our plots) were within the lower end of the range of those reported for other riverine systems, which span from 324 g C m⁻² yr⁻¹ to 1068 g C m⁻² yr⁻¹ (Brinson et al. 1990; Clawson et al. 2001). Lower ANPP values for arid, high-elevation western riparian ecosystems are likely due to a combination of factors, including highly variable stream flows, low and highly variable precipitation, short growing seasons, low relative humidity (causing reduced stomatal conductance when water is limiting), and the low water storage capacities and nutrient availabilities of the poorly developed soils they occupy (Smith et al. 1991; Adair and Binkley 2002). Nevertheless, stand-level leaf area indices

were moderate relative to values reported for upland temperate deciduous and evergreen forests (Landsberg and Gower 1997; Waring and Running 1998).

Our calculated estimates of BNPP (which includes all plants) were similar statistically between sites. Some studies in upland forests suggest that the relative allocation of total production belowground is higher in sites with greater belowground resource constraints on production, such as water stress and low nutrient supply (Keyes and Grier 1981; Gower et al. 1992; Runyon et al. 1994; Haynes and Gower 1995; Landsberg and Gower 1997; Raich 1998). Our results do not support this hypothesis given that BNPP:total NPP ratios from our sites (≈ 0.5) were at the high end of the range reported for these upland forests (0.2 to 0.6), and our assumption that at least one belowground resource, water, would be more readily available in riparian than in upland forests. In one of the few studies that have assessed both BNPP and ANPP in a riparian forest, Clawson et al. (2001) reported that the BNPP:total NPP ratio did increase as water availability declined in a floodplain forest of the southeastern U.S.. However, they also reported surprisingly low BNPP:total NPP ratios in these floodplain forests across all sites (from 0.03 to 0.13). Apparently, riparian forests may exhibit even greater variation in the patterns of C allocation across sites than has been found for upland forests.

Analyses of ecosystem functional attributes, like NPP, can be difficult due to the high-degree of spatial and temporal heterogeneity inherent within ecosystems, as well as the number of ecosystem components that need to be assessed to generate system-level measures. We conducted power analyses (two-tailed t-test, $P < 0.05$; Zar 1998) to estimate how many plots per site would be required to detect significant differences in 1999 for some of the productivity measures that did not show differences (assuming that differences did indeed exist). Based on these analyses, we would have needed 5 plots per site for ANPP, 25 plots for BNPP and 9 plots for total NPP in order to detect a significant difference between these sites. This result clearly illustrates the difficulty of measuring belowground and total NPP in these ecosystems. We believe, like many other researchers (Gregory et al. 1991; Muller et al. 2000), that ecosystem-level studies of riparian zones provide a rigorous ecological basis for evaluating ecosystem health, identifying management objectives, evaluating current management practices, and the development of future management plans. However, our results suggest that the only productivity measure likely to provide a sensitive, cost-effective index for evaluating the effect of stream flow diversion on western montane riparian areas is understory ANPP.

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EFFECTS OF THE NON-NATIVE GRASS, *PARAPHOLIS INCURVA*
(POACEAE), ON THE RARE AND ENDANGERED HEMIPARASITE,
CORDYLANTHUS MARITIMUS SUBSP. *MARITIMUS* (SCROPHULARIACEAE)

MEGHAN Q. N. FELLOWS

Natural Resource Management and Protection, Fairfax County Park Authority,
12055 Government Center Parkway, Suite 936, Fairfax, VA 22035
mnoefe@fairfaxcounty.gov

JOY B. ZEDLER

Department of Botany, University of Wisconsin, Madison, WI 53706

ABSTRACT

We tested the host efficiency of an abundant non-native annual grass *Parapholis incurva* for the rare and endangered hemiparasite *Cordylanthus maritimus* subsp. *maritimus*. Flower production in *C. m. maritimus* was significantly less when *P. incurva* was the sole host (average 1 flower), than when the native perennial grass host, *Distichlis spicata*, was present (average 13 flowers). When *C. m. maritimus* was prevented from parasitizing either the native or non-native host, flower production results were similar to that of the non-native host (average 1 flower). Formation of haustoria did not differ between host identity treatments (average 270 haustoria per pot), but was significantly less in treatments that did not allow root contact between the host and hemiparasite (average 10 haustoria per pot). The “pseudo-host” effect of the non-native annual grass could result in high energetic cost to the endangered hemiparasite. Management decision-makers should factor in the costs of non-competitive mechanisms when prioritizing non-native species removal in areas with rare hemiparasites.

Key Words: non-native invasives, endangered, salt marsh, hemiparasite, haustoria.

If non-native species become abundant, they can significantly disrupt community structure and alter ecosystem function (Vitousek and Walker 1989; D’Antonio and Vitousek 1992; Fiedler and Ahouse 1992; Schmitz and Simberloff 1997; Wilcove et al. 1998). Three mechanisms by which non-native species affect ecosystems have been identified by Vitousek (1990), namely, resource sequestration, trophic alterations and disturbance-regime alterations (reviewed in D’Antonio and Vitousek 1992). However, with the exception of introduced top predators, species-specific effects of non-native on native species are infrequently documented, especially for plants (Lawler et al. 2002). Species that are rare as a result of habitat requirements, density constraints, or geographic limitation (Rabinowitz 1986; Fiedler and Ahouse 1992; Gaston 1994) may be especially susceptible to increased pressure from invasive species (Table 1). Endemic and parasitic plant species may be even more vulnerable, due to their very specific habitat requirements (Marvier and Smith 1997). California alone has more than 1500 endemic plant species (Raven and Axelrod 1978) and 165 parasitic plant species (Skinner and Pavlik 1994). The United States has 687 native parasitic plant taxa, of which 309 are considered rare on the state level (Kartesz 1999). One of these is the focus of our research.

We examined the novel plant-plant relationship of a non-native invasive grass, *Parapholis incurva* (L.) C.E. Hubbard, and a rare and federally endangered hemiparasite, *Cordylanthus maritimus* Nutt.

ex Benth. subsp. *maritimus*. Both are annuals that occur in close proximity in the high-intertidal habitats of southern California’s coastal salt marshes. San Diego Bay, an international seaport with a Mediterranean-type climate, is especially susceptible to non-native species introductions. In its tidal marshes alone, 11 of 46 plant species are non-native (Sullivan and Noe 2000). In the 1996 and 1997 growing seasons, non-native species made up 36% and 40% of the seedlings, respectively, in the high-marsh habitat at Sweetwater Marsh National Wildlife Refuge (SWM) on San Diego Bay (Noe and Zedler 2001). The annual, *P. incurva*, dominated the seedling assemblage at SWM, comprising 26% and 18% of the total (Noe and Zedler 2001). At nearby Tijuana Estuary, *P. incurva* was the only non-native species that germinated in study plots, comprising 92% of seedlings in 1996 and 57% in 1997 (Noe and Zedler 2001). The abundance of non-natives in these marshes may increase as watersheds become increasingly urbanized and storm water runoff lowers the soil salinity and changes the structure and function of the downstream salt marsh (Kuhn and Zedler 1997; Callaway and Zedler 1998).

Rare marsh species may be negatively affected by the abundance of non-native plants. *Cordylanthus maritimus* subsp. *maritimus* has very limited geographic, habitat and community requirements that influence germination, establishment, survival and reproduction (Fig. 1) (Parsons and Zedler 1997; Fellows 1999; Noe and Zedler 2000). During 1996

TABLE 1. ATTRIBUTES OF *CORDYLANTHUS MARITIMUS* SUBSP. *MARITIMUS* THAT RELATE TO FIEDLER AND AHOUSE’S (1992) LIST OF CAUSES OF INTRINSIC RARITY. ¹ Parsons and Zedler 1997, ² Fink and Zedler 1989a, ³ Chuang and Heckard 1973, ⁴ Flick and Cayan 1985, ⁵ Helenurm and Parsons 1997, ⁶ PERL personal observation, ⁷ D. McIntire personal communication, ⁸ Mudie et al. 1976.

| Causes of rarity | <i>Cordylanthus maritimus</i> subsp. <i>maritimus</i> |
|-----------------------|--|
| taxon ecology | restricted to upper tidal marsh ¹ |
| life history strategy | non-host specific annual hemiparasite ^{2,3} |
| stochasticity | interannual fluctuations in rain, ENSO events ⁴ |
| reproductive biology | inefficient selfer, pollinator dependent ¹ |
| taxon genetics | low variability ⁵ |
| population dynamics | colonies fluctuate in number and location ⁶ |
| coevolution | dependent predator, evidence for pollinator ^{1,7} |
| earth history | youngest salt marshes only 2000 years old ⁸ |

and 1997, mean *C. m. maritimus* seedling abundance was only 3 and 2% of the all seedlings in the high-intertidal marsh at SWM and 7 and 9% at Tijuana Estuary (Noe and Zedler 2001). Historically, *C. m. maritimus* populations have fluctuated in response to changing environmental conditions. In a northern population of *C. m. maritimus* (Carpinteria Marsh), abundance ranged from one to over 10,000 individuals in a 27-year period (Chuang and Heckard 1973; W. Ferren, personal communication). An eight-year (1991–1998) monitoring effort at SWM recorded 10-fold variation in the abundance of a re-

established population, as well as spatial shifts in its location (Zedler et al. 1995; Parsons and Zedler 1997; Zedler et al. personal observation). The fluctuations (from 14,000+ individuals to less than 1400 individuals) led us to question the population’s sustainability and examine the factors that may influence its population dynamics. Non-native species have become more frequent in locations with *C. m. maritimus*, and although monitoring data do not allow us to draw conclusions about cause and effect, the observation is suggestive of a negative impact on the endangered species.

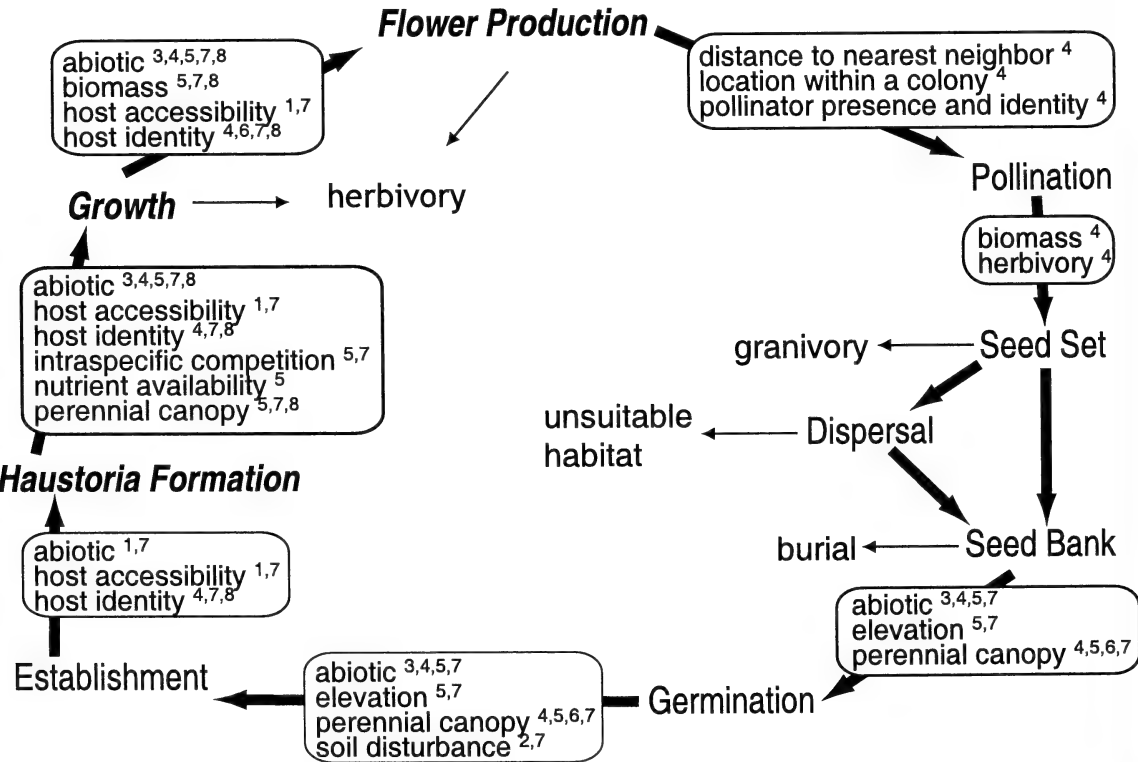


FIG. 1. Life processes of *Cordylanthus maritimus* subsp. *maritimus* and important and hypothesized important environmental factors. Non-native species are thought to influence processes indicated in bold and italics. ¹Chuang and Heckard 1971, ²Cox and Zedler 1986, ³Fink and Zedler 1989, ⁴Fink and Zedler 1990, ⁵Parsons and Zedler 1997, ⁶Vanderwier and Newman 1984, ⁷Fellows 1999, ⁸this study.

Cordylanthus maritimus subsp. *maritimus* is a facultative hemiparasite (Chuang and Heckard 1971; Chuang and Heckard 1973; U.S. Fish and Wildlife Service 1984). Hemiparasitic plants, although able to photosynthesize, use haustoria (secondary roots) to attach to a host plant (Kuijt 1969). Haustoria generally function by providing water and/or nutrients to the hemiparasite (Piehl 1966; Kuijt 1969; Chuang and Heckard 1971); we know of no specific studies of haustoria function in *C. m. maritimus*. Haustoria in *C. m. maritimus* may be induced as early as the cotyledon stage, probably in response to physical cues in the environment (Chuang and Heckard 1971). Like most hemiparasites, *C. m. maritimus* growth is limited when none of its multiple host species is present (Fink and Zedler 1990). Almost all common tidal marsh plants within the elevation range of *C. m. maritimus* have been suggested as suitable host species, including perennial grasses (e.g., *Distichlis spicata* (L.) Greene, *Monanthochloe littoralis* Engelm.), perennial sub-shrubs (e.g., *Salicornia virginica* (L.)) and non-native annuals (e.g., *Polypogon monspeliensis* (L.) Desf.) (Vanderwier and Newman 1984; Fink and Zedler 1990). However, few studies have tested the mechanism for differential response of *Cordylanthus* species to its hosts (Fink and Zedler 1989; Marvier 1998). In the tidal marsh, the life-span of most annuals, including non-native grasses like *P. incurva*, is out of synchrony with *C. m. maritimus*. While most annuals in the high-intertidal marsh senesce at the beginning of the dry season in early summer (May–June), *C. m. maritimus* initiates reproductive activity around May, peaking in July or August and may continue flowering until late September, suggesting annual species would probably not be suitable hosts. Host function during the hot and dry summer is critical for support of *C. m. maritimus*; therefore, the ability of a species to host *C. m. maritimus* needs to be tested under multiple seasonal conditions.

Cordylanthus maritimus subsp. *maritimus* has many natural constraints on its life cycle that contribute to its rarity (Fig. 1). The addition of a non-native species, such as *P. incurva*, could affect survivorship and reproduction of *C. m. maritimus*. The nature of this interaction is unknown. To assist managers in developing strategies for the recovery of *C. m. maritimus*, we explored the effects of different hosts under both wet and dry seasonal conditions.

METHODS

Biological Materials

Cordylanthus maritimus subsp. *maritimus* (*Cmm*) seeds were collected in 1995 from Tijuana River National Estuarine Research Reserve (U. S. Fish and Wildlife Service Collecting Permit #PRT 823806, Ca. 96-01-RP) and stored until December 1996 in a cool, dry environment. Seeds were cold

treated at 4°C in January 1997 until November 1997 and then sowed directly into the experimental unit. Germination tests prior to the beginning of the experiment had 84% germination on wet filter paper (fresh water (0% salt)) in petri dishes in a growth chamber (13 h light: 11 h dark, 17°C).

In January 1997, cuttings of unknown aged *Distichlis spicata* (*Ds*) (a known host for *C. m. maritimus* (Fink and Zedler 1990)) were salvaged from a small area of Tijuana Estuary that was slated for excavation. *Distichlis spicata* is one of several hosts in southern California salt marshes and co-occurs with most *C. m. maritimus* populations. Cuttings were allowed to root in one of 18 propagation flats with well-watered, 2:1:1 perlite: vermiculite: top soil mixture with additions of vitamin B₁₂ to encourage root growth. Cuttings that had rooted by June 1997 were transplanted into experimental pots by haphazardly selecting the pot and haphazardly selecting one cutting from a randomly chosen propagation flat. *Parapholis incurva* (*Pi*) is also present in most San Diego County salt marshes, co-occurring with *C. m. maritimus*, *Distichlis spicata* and other *C. m. maritimus* hosts. Seeds were collected in 1997 from two areas of Tijuana Estuary. Seeds were stored at 4°C for 6 months, soaked for 24 hours in water purified by reverse osmosis and then sowed directly into the experimental unit in July 1997.

Experimental Approach

The effect of *P. incurva* on *C. m. maritimus* was tested in an outdoor pot experiment at San Diego State University, using a complete two × three factorial design with two levels of water availability and three host treatments (*Pi*, *Ds*, and *Pi+Ds*), with five replicates per treatment (Fig. 2). Salinity was not included as a factor because none of the taxa are obligate halophytes and constant soil salinities are notoriously difficult to control in greenhouse conditions. Water baths maintained either 'watered' (water level at or near top of bath) or 'drought' (water drained from bath, until dry) treatment conditions. Each bath held one replicate of each host treatment. Because of the much smaller biomass of the non-native grass, we attempted to constrain initial host stem number to be constant across treatments, regardless of plant number. This resulted in host densities consisting of two to four plants of *P. incurva* (*Pi*), one plant (one or two root nodes) of native *D. spicata* (*Ds*), and up to five plants in *Pi+Ds*, maintaining the same density as when grown alone (i.e., *Pi+Ds* treatments had twice the number of stems). Each pot also contained one *C. m. maritimus* that had been haphazardly thinned from seedlings that germinated from directly sown seed.

A second experiment, run concurrently, tested the belowground effects of the hosts and the hemiparasite. The complete two × three factorial design had two water availability levels and three host accessibility treatments (*Cmm* alone (i.e., no host),

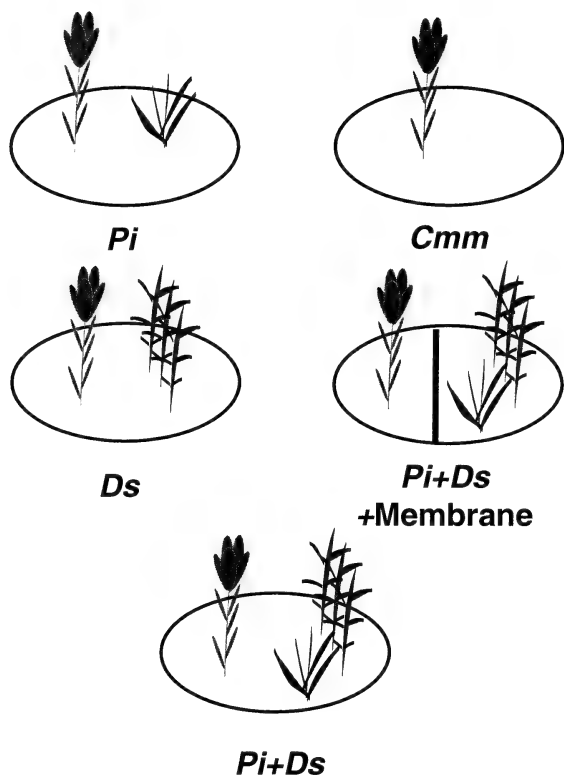


FIG. 2. Experimental design for host interaction tests. Treatments included *Parapholis incurva* (Pi only), *Distichlis spicata* (Ds only) or both (Pi+Ds) and *Cordylanthus maritimus* ssp. *maritimus* (Cmm only), both hosts separated by a membrane (Pi+Ds+Membrane) or both hosts (Pi+Ds).

Pi+Ds+Membrane (i.e., no root connection), and Pi+Ds) (Fig. 2). Water baths maintained treatment conditions as above. In pots with hosts and Cmm, the same number of stems was maintained in this experiment as the first experiment. A 30- μ m mesh membrane was buried in pots of Pi+Ds+Membrane that allowed water and nutrient movement but no haustorial connection between *C. m. maritimus* and its potential hosts.

For both experiments, the experimental unit was a tall pot made out of a 90-cm section of drain pipe (8-cm diameter), sealed at the bottom with felt, filled with sand to within 5-cm of the top, and planted with the appropriate host propagules and a *C. m. maritimus* seedling. Pots were kept upright in a frame under a clear plastic canopy to exclude rain. As there were no obvious environmental differences within the 0.6 \times 3.2-m experimental site, the units were kept in their original random locations. The experiments ran for eight months, from November 1997 to June 1998.

Pots were monitored twice a month until *C. m. maritimus* appeared to have reached maximum flowering, a minimal number of plants had senesced, and a natural eight-month, lifespan had tran-

spired. The two hosts were in variable condition with most of the annual host, *P. incurva*, recently senescent while the perennial host, *D. spicata*, appeared healthy. Flower number and haustoria number of *C. m. maritimus* were counted once, at the termination of the experiment. Root material was separated from the sand by spraying water over a 0.03-mm mesh screen. Roots of both host and hemiparasite were hydrated and examined for haustoria visible to the unaided eye (typical haustoria are 2 mm in diameter). Seed number was not monitored because suitable pollinators were not expected to be present at the location of the experiment, therefore seed production would be artificially low (Parsons and Zedler 1997). Organic material was separated by species for aboveground and, when possible, belowground biomass. Biomass of each component was dried at 60°C until constant weight and measured.

A two-way analysis of variance was used to test the significance of water level and host identity (or host accessibility) as main, categorical effects (SYSTAT 1992). Flower and haustoria number were log-transformed to improve the fit of the data to the assumptions of the analysis of variance. Multiple comparisons of flower and biomass data were performed with Tukey's post-hoc test (SYSTAT 1992). Survival data could not be statistically analyzed because categorical counts were less than five, and in some cases zero (SPSS 1999, Multinomial Logit Model; Ott 1992).

RESULTS

The non-native annual *Parapholis incurva* supported less flower production in the hemiparasite than the native perennial *Distichlis spicata* (Fig. 3A). *Cordylanthus maritimus* subsp. *maritimus* grown with *D. spicata* had twelve times as many flowers than when grown with *P. incurva* (Tukey's HSD Pi vs. Ds $P = 0.020$, Pi vs. Pi+Ds $P = 0.042$; $F = 11.492$, $P \leq 0.001$) (Fig. 3A). Haustoria number ($F = 0.591$, $P = 0.562$) did not show a significant effect of host species identity, but there was much variability (Fig. 3B). Survival data are presented but not statistically analyzed (Fig. 3C). Significance of results did not differ when calculated per experimental unit or per surviving *C. m. maritimus* individual. There was a strong correlation between *C. m. maritimus* flower number and dry-weight biomass ($r = 0.834$, $P \leq 0.001$).

Water treatment did not affect *C. m. maritimus* flower number; watered plants averaged 10.0 ± 2.8 flowers (mean ± 1 SE), while those undergoing drought averaged 9.1 ± 2.8 flowers ($F = 0.003$, $P = 0.96$) (Fig. 3A). Drought treatment may have stimulated haustoria production (Fig. 3B), as watered pots had a mean of 131.9 ± 27.8 haustoria per pot as compared to 269.2 ± 59.5 for drought-treated pots ($F = 3.336$, $P = 0.080$). There was no interaction between water treatment and host treatment for either flower or haustoria number.

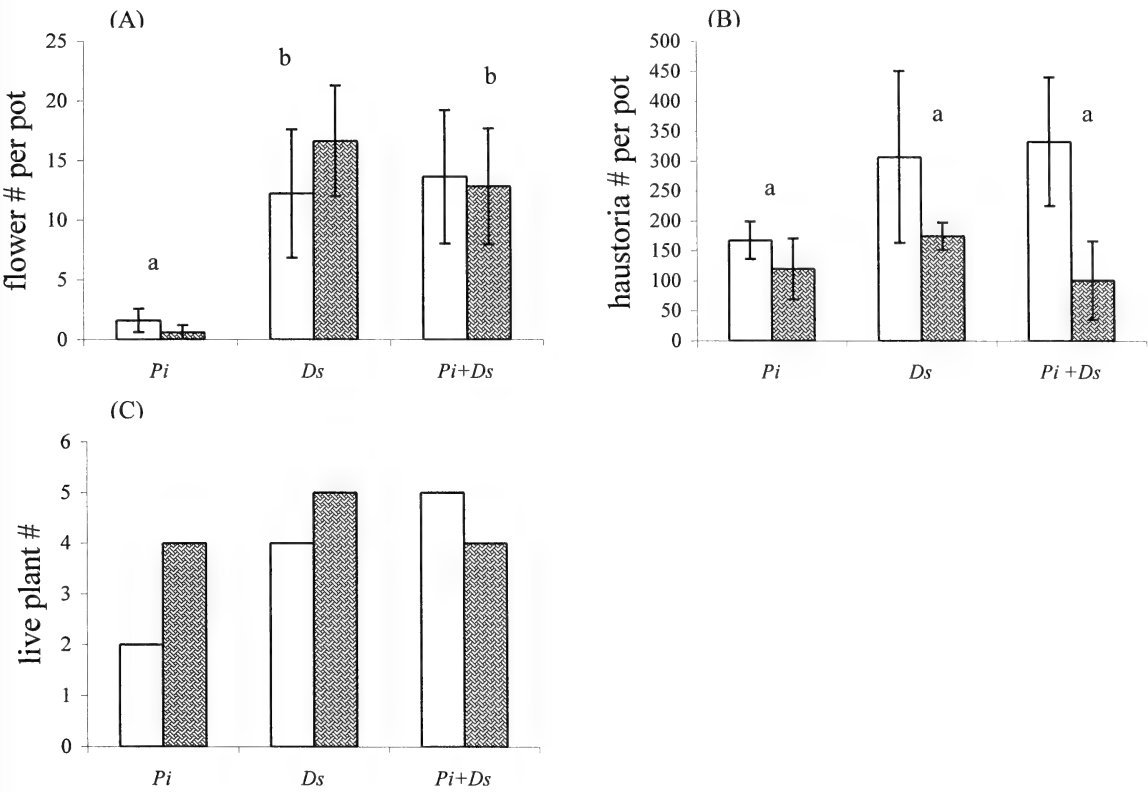


FIG. 3. Responses of *Cordylanthus maritimus* subsp. *maritimus* to three host identity treatments. A. Number of flowers per pot; B. Number of haustoria per pot; C. Survival through the eight-month experiment ($n = 5$, with one plant/pot; not analyzed statistically due to low n). Small letters signify differences ($p \leq 0.001$); error bars are ± 1 SE. Open bars are treatments with simulated drought. Abbreviations are defined in Figure 2 caption.

Biomass in pots with *D. spicata* was greater than in pots with the non-native *P. incurva* alone. *Parapholis incurva* in pots with both hosts had half as much aboveground biomass (*Pi+Ds*: 0.25 ± 0.03 g per pot) as when grown alone (*Pi*: 0.56 ± 0.07 g per pot) ($F = 40.116$, $P \leq 0.001$). *Distichlis spicata* biomass was unaffected by *P. incurva* presence (*Pi+Ds*: 0.74 ± 0.12 g per pot vs. *Ds*: 0.83 ± 0.09 g per pot; Tukey's HSD $P = 0.758$). Below-ground biomass was also much greater in treatments that included *D. spicata* (*Pi*: 0.303 ± 0.04 , *Ds*: 2.196 ± 0.24 , *Pi+Ds*: 2.555 ± 0.54 (all g per pot); Tukey HSD *Pi* vs. *Ds*: $P = 0.002$ and *Pi* vs. *Pi+Ds*: $P \leq 0.001$). Water treatment did not affect the biomass of the host shoots (*Ds*: $F = 2.53$, $P = 0.124$, *Pi*: $F = 1.37$, $P = 0.25$) or roots ($F = 1.119$, $P = 0.300$).

Restricting accessibility of host roots to *C. m. maritimus* with a fine pore membrane negatively affected *C. m. maritimus* flower number. Flower production averaged 17.5 ± 5.4 in *Pi+Ds* pots but only 1.0 ± 0.7 flower in *Cmm* or *Pi+Ds*+Membrane pots (Fig. 4A) (log transformed, $F = 15.33$, $P \leq 0.001$). Pots had 20 times as many haustoria in the *Pi+Ds* treatment than in either *Cmm* alone (Tukey's HSD $P \leq 0.001$) or *Pi+Ds*+Membrane (Tukey's HSD $P = 0.003$) ($F = 43.22$,

$P \leq 0.001$) (Fig. 4B). Survival of *C. m. maritimus* was very low in the *Pi+Ds*+Membrane treatment, with just two of the original 10 plants alive at experiment termination (Fig. 4C).

As in the first experiment, flower number was unaffected by water treatment ($F = 0.06$, $P = 0.81$) (Fig. 4A) and there was no water and host accessibility interaction ($F = 0.21$, $P = 0.810$). Again, haustoria production was unaffected by watering ($F = 0.38$, $P = 0.54$), although there was a significant interaction with host accessibility ($F = 3.02$, $P = 0.07$) (Fig. 4B).

Host aboveground biomass was greater in pots with a host present, of course, but unaffected by exclusion of root contact with the hemiparasite ($F = 24.794$, $P \leq 0.001$; *Pi+Ds*+Membrane: 0.59 ± 0.05 g per pot, *Pi+Ds*: 0.90 ± 0.15 g per pot, Tukey's HSD $P = 0.149$) or by water availability (watered: 0.55 ± 0.04 g per pot, drought: 0.41 ± 0.10 g per pot; $F = 0.67$, $P = 0.43$). Root biomass was greater in all pots with host roots ($F = 35.42$, $P \leq 0.001$; *Cmm* alone: 0.005 ± 0.001 g per pot, *Pi+Ds*+Membrane: 1.069 ± 0.166 g per pot, *Pi+Ds*: 2.138 ± 0.252 g per pot) although greater when roots were not excluded (Tukey's HSD *Pi+Ds*+Membrane vs. *Pi+Ds*, $P = 0.006$).

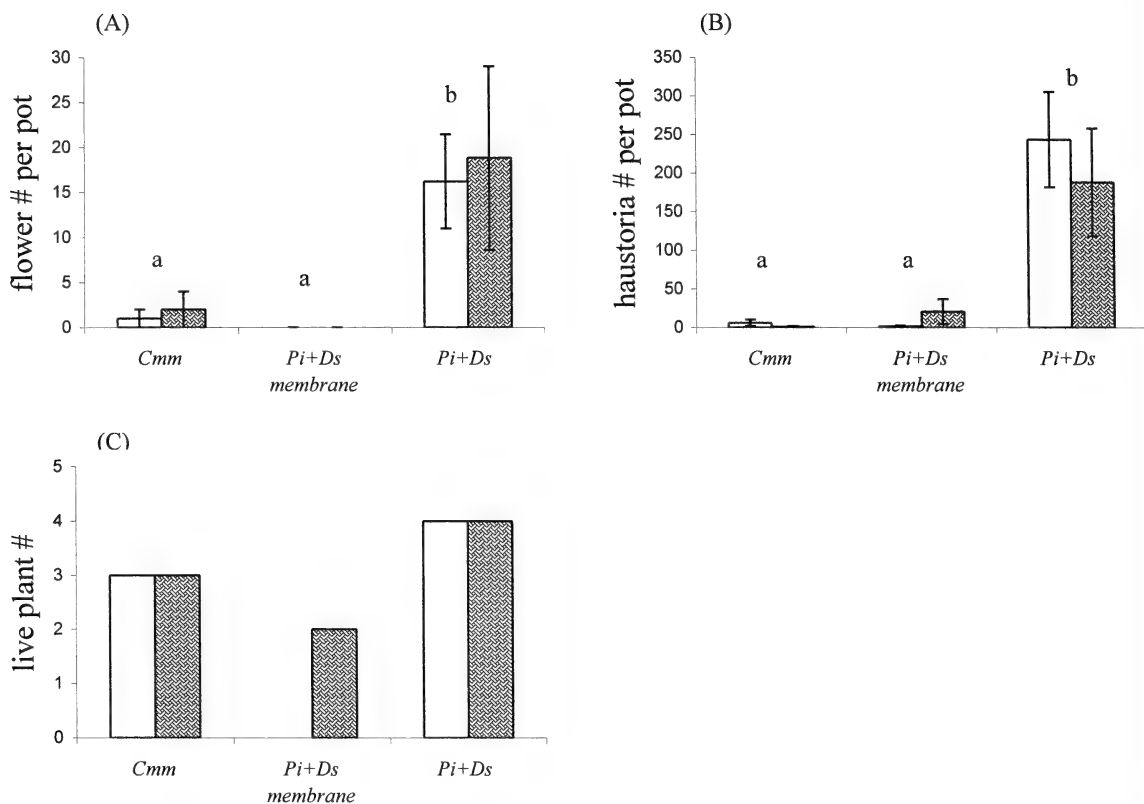


FIG. 4. Responses of *Cordylanthus maritimus* subsp. *maritimus* to three host availability treatments. A. Number of flowers per pot; B. Number of haustoria per pot; C. Survival through the eight-month experiment ($n = 5$, with one plant/pot; not analyzed statistically due to low n). Small letters signify differences ($p \leq 0.001$); error bars are ± 1 SE. Open bars are treatments with simulated drought. Abbreviations are defined in Figure 2 caption.

DISCUSSION

Effects of a Non-Native, Annual Host

The plant host-hemiparasite interaction may be affected by a multitude of factors, including: host health (Salonen and Puustinen 1996), abiotic stress (e.g., salinity, soil moisture, soil quality), hemiparasite density (parasite depression), and host density (intraspecific competition). Parasites show host preference by development of a cue/response system (i.e., chemical or physical); even "host generalists" exhibit a range of host preference (Kuijt 1969; Calladine et al. 2000) suggesting that not all hosts are equal. In this experiment, drought, lack of nutrient additions and high plant density all contributed to stressful conditions, so issues of comparative host health are not likely to be confounding in this study. Nutrient poor conditions are also typical of southern California salt marshes (Zedler et al. 1992), and were not seen as a significant stress on the experimental plants. Thus, we attribute results to the treatments, which included alternative hosts and limited host accessibility.

We showed that the endangered hemiparasite, *Cordylanthus maritimus* subsp. *maritimus* produced far fewer flowers when grown with the non-native

annual grass *Parapholis incurva* than with the native perennial host *Distichlis spicata* (Fig. 3A). Also, *C. m. maritimus* flower production was substantially reduced when a belowground host was unavailable (Fig. 4A). Haustoria production (as measured as final haustoria count), however, was similar when either host's roots were available, even though nearly no haustoria were produced when *C. m. maritimus* was grown alone.

Although we could not statistically test whether the non-native *P. incurva* host led to a premature death of *C. m. maritimus* individuals, the reduced flower production alone could decrease long-term sustainability of *C. m. maritimus* populations by depressing seed production. Further reducing reproductive potential, the abundance of *P. incurva* (e.g., the 91.5% of seedlings in *C. m. maritimus* habitat at Tijuana Estuary in 1996 (Noe and Zedler 2001)) could reduce *C. m. maritimus* population viability by decreasing the number of pollinator visits due to the smaller visual cue of a smaller number of flowers (Parsons and Zedler 1997). Reduced flower production defines a specific mechanism by which a non-native plant could decrease native plant function and sustainability in the natural ecosystem.

Haustoria Function

Haustoria function is rarely quantified (exceptions include Marvier 1998 and Calladine et al. 2000). One elegant technique to determine function is to measure the secondary compounds that may flow through the haustoria connection (e.g., Marvier 1998). More often, function is assumed if haustoria are observed to penetrate the host root (e.g., Calladine et al. 2000). Haustoria counts on 20 different potential native hosts of *Nuytsia floribunda* (Labill.) R.Br. did not strongly correlate with hemiparasite biomass, leading to the suggestion of a gradient of function based on species-specific anatomy or proportional exchange of organic solutes (Calladine et al. 2000). Although *P. incurva* might have affected the hemiparasite *C. m. maritimus* by preventing haustoria production, allowing the formation of anatomically non-functional haustoria or depressing the effect of properly functioning haustoria (either through the shorter-lived *P. incurva* senescence or a physiologic mechanism), we found no evidence of the first mechanism. A detailed anatomical study to determine if the visible haustoria were indeed penetrating the host roots and fully functional was beyond the scope of this ecologically-focused study. However, we do know that in both drought and well-watered conditions, the number of haustoria did not differ between host treatments (Fig. 3B). Hence, we attribute the reduced reproductive potential of *C. m. maritimus* to some level of reduced haustoria function, whether it is an anatomic failure, or merely a failure of the annual *P. incurva* to provide the necessary compounds to *C. m. maritimus*.

Production of functional haustoria can benefit the hemiparasite by increasing the amount of water and/or nutrients available to the plant. The trend of increased haustoria production observed in the drought treatments suggests that *C. m. maritimus* can respond to changing environmental conditions. Alternatively, the cost of a non-functioning haustorium, or one that operates at a reduced function, may be detrimental to the hemiparasite. Shedding of non-functional function-specific roots, is not unknown in the plant kingdom, e.g., rain induced roots (Hunt et al. 1987) or in response to lack of soil N (Burton et al. 2000). Although survivorship data could not be statistically analyzed, some mortality of *C. m. maritimus* individuals in the *Pi* treatment (Fig. 3C) could be one negative outcome of unsuccessful parasitism. A future study to determine the cost of producing non-functioning haustoria could define the potential negative impact of non-functional haustoria on growth and reproduction of *C. m. maritimus*.

Management Implications

A basic understanding of the ecology of rare species (Fig. 1) is needed before populations can be conserved, recovered, reintroduced, or introduced.

This is especially important when the ecosystem is being created from a different system or new land (e.g., wetlands from dredge spoils). Non-native species invasions are known to slow ecosystem restoration efforts (Callaway and Sullivan 2000). Others have focused on non-native species' effects on resources (e.g., sequestration of water or nutrients), altered trophic interactions (e.g., carnivory, herbivory, granivory) and alterations of disturbance regimes (e.g., fire frequency; reviewed by Vitousek 1990). To this list we add interference with parasite-host efficiency. For the over 3000 parasitic angiosperm species that depend on specific host attributes (Marvier and Smith 1997), non-native species may cause an additional hurdle by interrupting host plant-parasite interactions. A parasite that attaches to a host that cannot support it to the reproductive stage experiences direct interference. In effect, the non-native species is a "pseudo-host," allowing haustoria formation, but not necessarily contributing to the maintenance of the hemiparasite. The removal of abundant non-native species, and establishment of native host species would appear to be desirable for improving growth and flowering (and thus reproduction) of *C. m. maritimus*.

Non-native species are recognized as a primary cause of species endangerment, second only to habitat destruction (Schmitz and Simberloff 1997; Wilcove et al. 1998). Hence, managers need to create high quality habitats, free of non-native species. While management plans often call for the removal of invasive species for reasons of aesthetics, fire control, improved water management, or replacement of monocultures to increase biodiversity, our results suggest another subtle benefit, namely increased reproduction of rare parasitic plants.

ACKNOWLEDGMENTS

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GENETIC VARIATION IN EASTERN WASHINGTON POPULATIONS OF
NAVARRETIA LEUCOCEPHALA (POLEMONIACEAE)
A VERNAL POOL ENDEMIC

DAVID L. BOOSE¹, BENJAMIN R. HARMELING, AND ROGER T. TURCOTTE
Department of Biology, Gonzaga University, 502 East Boone Avenue,
Spokane, WA 99258

ABSTRACT

We used Random Amplified Polymorphic DNA (RAPD) to investigate genetic variation in eight populations of the vernal pool endemic *Navarretia leucocephala* Benth. in eastern Washington. Five of the populations were subspecies *minima*, collected in Spokane County. The other three populations were subspecies *diffusa*, a recently described taxon known only from adjacent Lincoln County in eastern Washington. We also sampled a nearby vernal pool population of *N. intertexta* (Benth.) Hook., a closely related species whose range overlaps with *N. leucocephala*. Distances among the sampled pools ranged from a few tens of meters to 80 km. The populations differed in their levels of genetic variation, with proportions of polymorphic loci ranging from 10% to 55% and mean gene diversities from 0.05 to 0.30. Analysis of Molecular Variance (AMOVA) among the eight *N. leucocephala* populations showed significant spatial structuring, with 52% of the observed genetic variation due to differences between the Spokane County and Lincoln County populations. Within each county, 10% – 34% of the genetic variation was due to differences among populations. Estimates of Φ_{ST} indicated significant population differentiation among all populations of *N. leucocephala* ($\Phi_{ST} = 0.65$), but the degree of differentiation varied with interpopulation distance. Populations 35–250 m apart were generally not differentiated. At a distance of 1100–1800 m, some populations showed significant differentiation and others did not. Populations 80 km apart were significantly differentiated. On a distance-based phenogram, *N. intertexta* separated clearly from the *N. leucocephala* populations, which also grouped by subspecies, suggesting that the morphological features used to differentiate the taxa are paralleled by genetic differences.

Key Words: Columbia Plateau, genetic differentiation, RAPD, *Navarretia*, Polemoniaceae, vernal pools.

Plants inhabiting ephemeral wetlands known as vernal pools are likely to show significant spatial structure in their genetic variation. Natural selection, restricted gene flow, and genetic drift can combine to create non-random distributions of genotypes at multiple spatial scales, with implications for the evolutionary trajectories of vernal pool species, and for efforts to preserve vernal pool biodiversity. Yet few experimental data exist on genetic variation within and among vernal pool populations (Elam 1998).

Vernal pools occur in regions with cool, wet winters and hot, dry summers. They form when winter rains fill depressions underlain by an impervious layer, then dry out during the spring and early summer, remaining dry for several months (Keeley and Zedler 1998). While vernal pools are most numerous in California, they also occur in the intermountain regions of several western states, including Oregon and Washington (Björk 1997), as well as Baja California, Mexico and areas of Argentina and Chile (Keeley and Zedler 1998). Pools generally show a highly clustered distribution, occurring in localized regions where the substrate and climate conditions allow their formation. Within these regions are “archipelagos” of pools a few meters to

a few hundred meters apart, separated from other such archipelagos by tens to hundreds of kilometers (Holland and Jain 1981). Most vernal pool plant species do not occur in the intervening uplands, so this structured distribution of habitat imposes a strongly patchy distribution of populations, among which genetic variation may develop.

Because vernal pools are filled primarily through precipitation, local soil and hydrologic factors have a strong influence on the conditions experienced by vernal pool plants (Keeley and Zedler 1998). These different chemical and hydrologic environments are likely to select for different physiological and life-history characteristics, resulting in divergent selection pressures among pools. Many vernal pool plant species are endemic not only to vernal pools, but to specific subtypes of pools, differentiated by local climate factors, soil types, and topographic position (Stone 1990; Alexander and Schlising 1998; Bauder and McMillan 1998).

The potential for divergence among vernal pools is enhanced by the restricted nature of gene flow in many vernal pool plants. Leong et al. (1995) found that pollinators foraged occasionally between vernal pool patches 25 m apart, but rarely among patches 80–100 m apart. Using fluorescent dyes to track pollen movements in vernal pool *Limnanthes* species, Thorp (1990) found that 97% of the dye was distributed within 5 meters of the source plants,

¹ Author for correspondence, email: boose@gonzaga.edu

with occasional dispersal up to 13 meters. In *Limnanthes douglasii* R. Br. subsp. *rosea* (Benth.) C.T. Mason, a vernal pool endemic, 85% of plants received pollen from donors within 10 cm, and fewer than 5% received pollen from as far away as 80 meters (Kesseli and Jain 1982). Seed dispersal distances in vernal pool plants are also expected to be highly skewed, with most seeds falling close to the maternal plant (Zedler 1990). For example, vernal pool species in the genus *Navarretia* have indehiscent fruits, retaining their seeds within the capsule until the pools fill the following winter or spring. Swelling of the moistened seed coats bursts the membranous capsule, resulting in extremely localized dispersal (Spencer and Spencer 2003). Seeds of vernal pool plants may spread through wind-driven water movements, but transport among pools is likely to be limited (Jain 1978). On the other hand, some long-distance transport of seeds obviously occurs, given the broad ranges of many vernal pool taxa, and the discontinuous nature of their habitat (Schleidlinger 1981).

The genus *Navarretia* includes 12 species and subspecies that are more or less restricted to vernal pools and other ephemeral wetlands throughout the western United States, and a single species found in similar habitats in Chile and Argentina (Spencer and Porter 1997; Björk 2002; Spencer and Spencer 2003). Several taxa are widely distributed throughout the West. For example, *N. leucocephala* Benth. occurs from the San Joaquin Valley in California north through Oregon and eastern Washington, and east into Idaho and Utah (Hitchcock et al. 1964; Day 1993). A closely related species, *N. intertexta* (Benth.) Hook., also occurs throughout much of the range of *N. leucocephala*. In contrast to *N. leucocephala*, *N. intertexta* is more of a habitat generalist, occurring in vernal pools, but also inhabiting moist uplands and meadows (Day 1993a).

Day (1993b) identified five subspecies of *N. leucocephala* based on morphological characteristics; recently a sixth subspecies, *N. leucocephala* subsp. *diffusa* Björk, was identified from vernal pools in the Columbia Plateau of eastern Washington (Björk 2002). The most common subspecies of *N. leucocephala* in eastern Washington is *N. leucocephala* subsp. *minima* (Nutt.) Day, which is widely distributed in the region. Subspecies *diffusa* and *minima* both occur in similar habitats in Lincoln county, but their ranges in the county do not overlap. Subspecies *diffusa* is not found elsewhere in the state (Björk 2002). The degree to which the morphological differences between these subspecies reflect molecular genetic variation is unknown. In a recent phylogeny of the genus (Spencer 1997), an analysis of 22 morphological characters failed to distinguish among five subspecies of *N. leucocephala* (subsp. *diffusa* was not included). Adding sequence data from the ribosomal RNA internal transcribed spacer (ITS) region separated *N. l. minima* from the other

four subspecies, but with little bootstrap support (Spencer 1997; Spencer and Porter 1997).

We used Random Amplified Polymorphic DNA (RAPD) markers to investigate genetic variation within and among populations of *N. leucocephala* from vernal pools in the Columbia Plateau of eastern Washington. RAPD markers (Williams et al. 1990) are a PCR-based indicator of genetic variation commonly used in studies of population genetics. RAPD markers are dominant, so heterozygotes cannot be directly distinguished from homozygotes at a particular RAPD locus. If populations are assumed to be in Hardy-Weinberg equilibrium, then the frequency of the "null" allele can be estimated as the square root of the frequency of the negative phenotype. If the assumption of Hardy-Weinberg equilibrium cannot be justified, then multilocus RAPD phenotypes can be treated as haplotypes, and genetic diversity and population differentiation can be estimated based on pairwise differences between individual haplotypes (Weising et al. 1995; Wolff and Morgan-Richards 1999).

Specifically, we sought to address the following two questions:

- 1) What is the current distribution of genetic variation among populations of *N. leucocephala* in eastern Washington?
- 2) Is the distribution of genetic variation concordant with the morphologically based subspecies designations of Björk (2002)?

METHODS

In eastern Washington, vernal pools occur in three distinct "tracts", running roughly from northeast to southwest, following the paths of Pleistocene floods that scoured off surface soils and exposed basalt bedrock (Fig. 1). Outside of these tracts, soils are too deep or too well-drained to support vernal pool formation (Björk 2002). We sampled eight populations of *N. leucocephala* from vernal pools in Spokane and Lincoln Counties. The three Lone Pine Road populations (L1–L3) are subsp. *diffusa*, collected in the Swanson Lakes Wildlife Area in Lincoln County (47.6°N, 118.5°W), in the central, "Davenport" tract (*sensu* Björk 2002). The other five populations (SN1, SN2, SS1–SS3) are subsp. *minima*, collected in the Turnbull National Wildlife Refuge in Spokane County (47.4°N, 117.5°W), in the "Cheney-Palouse" tract (*sensu* Björk 2002). Pools within each group were 20–1600 m apart; the Lincoln County populations are approximately 80 km distant from the Spokane County populations. To compare intraspecific variation to interspecific variation, we also sampled a population of *N. intertexta* occupying a small vernal pool located between the two SN populations.

From six to ten entire plants were collected from each population, with no two collected individuals closer than two meters apart. DNA was extracted from approximately 50 mg of stem and leaf tissue

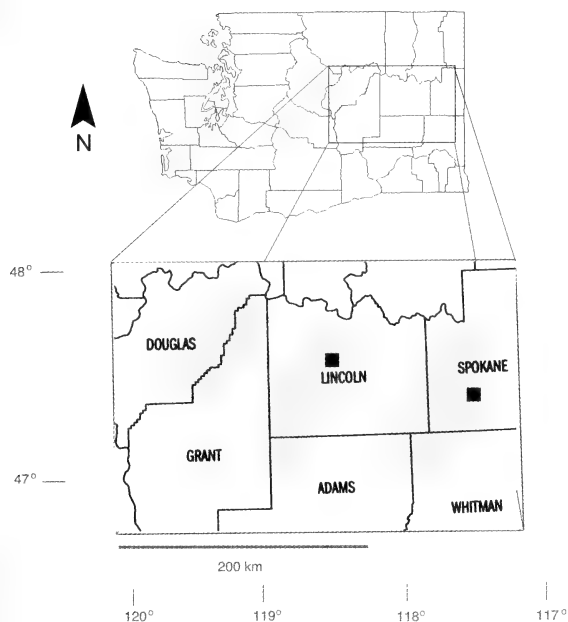


FIG. 1. Map showing locations of the *N. leucocephala* populations sampled for this study. Shaded areas indicate regions of vernal pool occurrence in Eastern Washington. Squares show locations of the sampled populations.

using the Wizard® DNA extraction kit manufactured by Promega Corporation (Madison, Wisconsin, USA), following the manufacturer's protocol. Genomic DNA was amplified with three 10-bp primers (Operon A1, A2, and A13), using RED-Taq® ReadyMix (10 mM Tris-HCl, 50 mM KCl, 1.5 mM MgCl₂, 0.001% gelatin, 0.2 mM dNTP, 0.75 u Taq Polymerase; manufactured by Sigma-Aldrich, St. Louis, Missouri, USA), with 100 ng template DNA, and 25 pmol primer in a 25 uL reaction. Reaction conditions consisted of 3 min at 95°C, followed by 45 cycles of 1 min at 95°C, 1 min at 35°C, and 2 min at 72°C, ending with a three minute final extension at 72°C. Amplification products were separated in 1.8% agarose gels and visualized by staining with ethidium bromide. Gels were recorded using a digital camera with a Tiffen deep yellow filter (#15). Each individual was amplified at least three times with each primer, and only strong bands appearing in at least two runs were scored as present. The three primers produced 11 reliably scorable loci, all of which were polymorphic, and which produced 42 different multilocus haplotypes in the 77 individuals sampled.

Statistical analyses were carried out using the software package Arlequin 2.0 (Schneider et al. 2000). For each population, we calculated the proportion of polymorphic loci, the mean number of pairwise differences among individuals across loci, and the average gene diversity (Nei 1987). Pairwise distances among all pairs of individuals (within and across populations) were computed as the number of different alleles between any two haplotypes.

This matrix of individual distances was then used to estimate measures of genetic structure through an Analysis of Molecular Variance (AMOVA; Weir and Cockerham 1984). We partitioned total genetic variance into three covariance components: between counties (Lincoln vs. Spokane), among populations within a county, and within populations. The significance of these partitions was evaluated using permutation tests based on 1,000 randomizations of the data for each level of partitioning being tested (Schneider et al. 2000). We also analyzed each county's populations separately, partitioning variation into among- and within-population components.

The inter-individual genetic distances were also used to calculate pairwise estimates of genetic differentiation (Φ_{ST}) among all nine sampled populations (Excoffier et al. 1992; Wright 1965; Weir and Cockerham 1984). Significance of the Φ_{ST} values was evaluated using permutation tests based on 3000 randomizations, and using Markov-based exact tests analogous to Fisher's exact test for 2×2 tables (Raymond and Rousset 1995; Schneider et al. 2000). Estimates of gene flow between populations (Nm) were calculated using the formula:

$$\Phi_{ST} = \frac{1}{\frac{4Nmd}{(d-1)} + 1}$$

where N is the population size, m is the proportion of the population migrating, and d is the number of demes exchanging genes (Slatkin 1991). Because the actual number of populations exchanging genes is unknown, we calculated the estimates with $d = 2$, as if the two populations being compared only exchanged genes with one another. This is unlikely to be true, but the gene flow estimates were meant to be for comparative purposes only, and not as reliable measures of actual migration among populations.

Pairwise Φ_{ST} values were also converted to estimates of genetic distance using the formula $D = \Phi_{ST}/(1 - \Phi_{ST})$ (Slatkin 1995), which produces a measure proportional to divergence time between the populations. These estimates were used to create a distance-based tree using the method of Fitch and Margoliash (1967) in PHYLIP (Felsenstein 1993).

RESULTS

The RAPD markers showed significant genetic variation within and among populations of *N. leucocephala* in eastern Washington. The 77 individuals sampled possessed 42 different multilocus haplotypes, 32 of which were found in only a single population. Across populations, the proportion of polymorphic loci ranged from 10% to 55%, and the average number of pairwise differences between individuals within a population ranged from 0.47 to 3.33 (Table 1). Average gene diversity (the proba-

TABLE 1. SAMPLE SIZE (n), NUMBER OF MULTILOCUS RAPD HAPLOTYPES, PERCENTAGE OF POLYMORPHIC LOCI (P_p) MEAN PAIRWISE DIFFERENCES AMONG INDIVIDUALS, AND MEAN GENE DIVERSITY IN EIGHT POPULATIONS OF *NAVARRETIA LEUCOCEPHALA* FROM EASTERN WASHINGTON.

| Population | n | Haplotypes (number unique) | P _p | Mean pairwise differences (±SD) | Mean gene diversity (±SD) |
|------------|----|-------------------------------|----------------|------------------------------------|------------------------------|
| L1 | 6 | 5 (4) | 36% | 1.80 ± 1.20 | 0.16 ± 0.13 |
| L2 | 6 | 6 (6) | 55% | 3.33 ± 1.99 | 0.30 ± 0.21 |
| L3 | 8 | 7 (6) | 60% | 2.57 ± 1.54 | 0.25 ± 0.18 |
| SN1 | 10 | 3 (0) | 10% | 0.47 ± 0.44 | 0.05 ± 0.05 |
| SN3 | 9 | 7 (4) | 45% | 1.89 ± 1.19 | 0.17 ± 0.12 |
| SS1 | 10 | 5 (2) | 36% | 1.47 ± 0.97 | 0.13 ± 0.1 |
| SS2 | 10 | 5 (3) | 36% | 1.56 ± 1.01 | 0.14 ± 0.10 |
| SS3 | 10 | 6 (4) | 55% | 2.38 ± 1.41 | 0.21 ± 0.14 |

bility that any two individuals drawn from the population will be different at a locus) ranged from 0.05 to 0.30. There was no geographic pattern to the distribution of within-population variation.

AMOVA results indicated significant genetic differentiation in *N. leucocephala* at all three levels analyzed (Table 2a). The majority of the variation (ca. 53%) was between the two counties, with most of the remainder (ca. 35%) found within populations. When the populations were analyzed separately by county, the majority of the variation was found to be within populations (Table 2b, c). In the Lincoln County populations, within-population variation accounted for 89.76% of the total, while in Spokane County, it accounted for 66.35%.

The overall Φ_{ST} value among all populations was 0.652 ($P < 0.001$), indicating a high level of differentiation. As in the AMOVA, much of this differentiation was due to differences between the two counties. When the two groups were analyzed separately, the Spokane County populations still showed significant differentiation ($\Phi_{ST} = 0.337$, $P < 0.001$), while differentiation among the Lincoln

County populations was marginal ($\Phi_{ST} = 0.103$, $P = 0.077$).

On a pairwise basis, Φ_{ST} values indicated significant differentiation between most pairs of populations (Table 3). Permutation tests and exact tests gave slightly different results for the significance of these pairwise Φ_{ST} values. In particular, six Φ_{ST} values found to be significant under the permutation tests were not significant at the 0.05 level according to the exact test (Table 3). Of these, the three involving population SS3 had p-values between 0.055 and 0.066 according to the exact test; the three involving population SN3 had exact test p-values ranging from 0.11 to 0.26. When pairwise Φ_{ST} values were converted to estimates of migration rates, the vast majority were below 0.5 migrants per year. Among the most similar populations, estimates ranged from 1 to 4 migrants per year (Table 3).

In the distance-based phenogram, populations clustered together geographically, with the Lincoln County populations (L1–L3) grouped in a clade separate from the Spokane County populations

TABLE 2. RESULTS FROM ANALYSIS OF MOLECULAR VARIANCE (AMOVA) ON EIGHT POPULATIONS OF *NAVARRETIA LEUCOCEPHALA* FROM EASTERN WASHINGTON. Results are based on 11 RAPD loci treated as multilocus haplotypes. a) All populations combined. b) Five Spokane County populations only. c) Three Lincoln County populations only.

| Source of variation | df | Sum of squares | % of variation | P |
|-----------------------------------|----|----------------|----------------|-------|
| a) All populations | | | | |
| Between counties | 1 | 44.997 | 52.59 | 0.02 |
| Among populations within counties | 5 | 24.055 | 12.60 | <0.01 |
| Within populations | 61 | 58.789 | 34.81 | |
| Total | 68 | 127.841 | 100.00 | |
| b) Spokane County populations | | | | |
| Among populations | 4 | 19.24 | 33.65 | <0.01 |
| Within populations | 44 | 35.46 | 66.35 | |
| Total | 48 | 54.69 | 100.00 | |
| c) Lincoln County populations | | | | |
| Among populations | 2 | 4.82 | 10.26 | 0.08 |
| Within populations | 17 | 23.33 | 89.74 | |
| Total | 19 | 28.15 | 100.00 | |

TABLE 3. PAIRWISE Φ_{ST} VALUES (ABOVE DIAGONAL) AND CORRESPONDING ESTIMATED NUMBER OF MIGRANTS PER GENERATION, NM (BELOW DIAGONAL), AMONG EIGHT POPULATIONS OF *NAVARRETIA LEUCOCEPHALA* BASED ON 42 MULTILOCUS RAPD HAPLOTYPES. Bold type indicates Φ_{ST} values significantly different from zero at $P < 0.05$. Asterisks indicate Φ_{ST} values found to be significant under permutation tests, but not under exact tests.

| | L1 | L2 | L3 | SN1 | SN3 | SS1 | SS2 | SS3 |
|-----|------|-------|-------|--------------|---------------|--------------|--------------|---------------|
| L1 | | 0.175 | 0.094 | 0.841 | 0.735* | 0.718 | 0.715 | 0.625 |
| L2 | 1.18 | | 0.058 | 0.742 | 0.633* | 0.565 | 0.568 | 0.382* |
| L3 | 2.40 | 4.02 | | 0.708 | 0.585* | 0.542 | 0.552 | 0.423* |
| SN1 | 0.05 | 0.09 | 0.10 | | 0.000 | 0.485 | 0.444 | 0.519 |
| SN3 | 0.09 | 0.15 | 0.18 | — | | 0.393 | 0.361 | 0.428* |
| SS1 | 0.10 | 0.19 | 0.21 | 0.27 | 0.39 | | 0.067 | 0.085 |
| SS2 | 0.10 | 0.19 | 0.20 | 0.31 | 0.44 | 3.47 | | 0.220 |
| SS3 | 0.15 | 0.40 | 0.34 | 0.23 | 0.33 | 2.70 | 0.89 | |

(Fig. 2). Within the Spokane County populations, populations SN1 and SN3 are genetically indistinguishable, yet significantly differentiated from the three SS populations. As expected, the population of *N. intertexta* falls outside the clade that includes all eight *N. leucocephala* populations, despite the fact that it is less than 300 meters from population SN3, and less than 1700 meters from the SS populations.

DISCUSSION

Expectations for genetic variation in vernal pool plants will depend on the life-history of the species involved (Elam 1998). Among plants in general, annual species have been found to have lower within-population genetic diversity than perennials, based on allozyme (Hamrick and Godt 1989) or DNA markers (Nyblom 2004). Summarizing 60 studies of wild plant populations using RAPD analysis, Nyblom (2004) found an overall mean gene diversity of 0.22 ± 0.12 . Thus the amount of genetic variation within populations of *N. leucocephala* (mean gene diversity: 0.18 ± 0.08) appears

to be comparable to that for other annual plants in general.

Within-population genetic diversity will also depend on the balance between opposing evolutionary and ecological processes. On one hand, isolation and genetic drift could lead to reduced within-population diversity. In contrast, self-incompatibility and long-lived seed banks could work to maintain significant diversity (Baker 1989; Hairston et al. 1996; Nunney 2002). All of the sampled *N. leucocephala* populations are quite large, with population sizes in the thousands of individuals. Thus, genetic drift is not expected to have a strong effect on within-population diversity, compared to other evolutionary forces. While the mating system of *N. leucocephala* is not known from experimental studies, pollen:ovule ratios suggest that it is primarily outcrossing (Cruden 1977; Plitmann and Levin 1990; Spencer 1997). Information on the seed bank is also unavailable, but the ephemeral, variable conditions in vernal pools favor the development of seed dormancy, and such dormancy is common among vernal pool plants (Elam 1998). These factors would tend to favor the maintenance of significant genetic diversity in populations of *N. leucocephala*.

The level of gene diversity we observed in *N. leucocephala* is comparable to that seen in RAPD studies of plants with predominantly selfing or mixed breeding systems. Nyblom (2004) reported average gene diversities of 0.12 over ten predominantly selfing species, and 0.18 in eight species with mixed mating systems. Both of these values were significantly lower than the average of 0.27 for 38 predominantly outcrossing species (Nyblom 2004). Thus, while pollen:ovule ratios may indicate a tendency for outcrossing in *N. leucocephala*, levels of genetic diversity suggest that selfing or mating among close relatives may be frequent in these populations. Because of the limited seed dispersal distances in *N. leucocephala*, plants often occur in clumps of many individuals in very close proximity. Members of these clumps are likely to be at least half-sibs, so pollinator movements among adjacent plants could result in significant inbreeding.

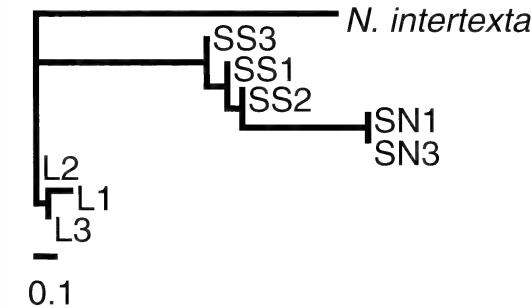


FIG. 2. Phenogram showing relationships among eight populations of *Navarretia leucocephala* and one population of *N. intertexta* in eastern Washington. Populations L1, L2, and L3 are subspecies *diffusa* from Lincoln County; populations SS1, SS2, SS3, SN1 and SN3 are subspecies *minima* from Spokane County, approximately 80 km distant. The population of *N. intertexta* was collected approximately 300 m from population SN3. Distances are Slatkin's linearized distances, calculated from 11 RAPD loci analyzed as multilocus haplotypes.

When all populations were considered together, *N. leucocephala* showed levels of population differentiation comparable to those found in RAPD studies of other annual plant species. Nybom (2004) reported a mean Φ_{ST} value of 0.62 across ten such studies, quite close to the value of 0.65 we calculated for *N. leucocephala*. But much of the differentiation we observed can be attributed to differences between the Spokane County and Lincoln County populations; separate analyses of these groups produce lower levels of differentiation. The Spokane County populations exhibit greater differentiation ($\Phi_{ST} = 0.337$) than the Lincoln County populations ($\Phi_{ST} = 0.103$), probably due to the smaller number and closer proximity of populations sampled in Lincoln County. In general, Φ_{ST} values based on RAPDs tend to increase with increasing interpopulation distances (Nybom 2004).

The Spokane County populations exhibit a level of differentiation similar to that seen in other RAPD studies of plants with mixed mating systems. Nybom (2004) reported an average Φ_{ST} of 0.40 for 18 such species, less than that seen for predominantly selfing species (mean $\Phi_{ST} = 0.65$; $N = 14$), and greater than the average for outcrossing species (mean $\Phi_{ST} = 0.27$; $N = 73$). Differentiation among the Spokane county populations is also higher than that found in most other studies of vernal pool plants, but this may be a result of the different markers used. Allozyme data from six vernal pool plant taxa, in two genera, showed F_{ST} values ranging from 0.083 to 0.176 (Elam 1998). A seventh taxon, *Limnanthes floccosa* Howell subsp. *californica* Arroyo had an F_{ST} value of 0.963, indicating extreme genetic differentiation among populations (Dole and Sun 1992; Elam 1998). The higher Φ_{ST} values we observed among *N. leucocephala* populations may result in part from greater variability of RAPD markers compared to allozymes. Hamrick and Godt (1989) reported an average F_{ST} value of 0.357 ± 0.024 for annual plant populations based on allozyme variation, compared to the average Φ_{ST} value of 0.62 reported by Nybom (2004) for annual plants using RAPD data.

The pairwise F_{ST} values observed in this study suggest that gene flow between pools a few hundred meters apart is generally sufficient to prevent differentiation. As a general rule, genetic drift can lead to differentiation between two populations if the number of migrants between them (Nm) is less than one per generation (Slatkin 1987). The three SS populations are all less than 100 m from one another, and show low to insignificant levels of differentiation and estimated Nm values between 0.89 and 3.5 (Table 3). Similarly, the three Lincoln County populations are separated by 35–250 m, and show no significant differentiation. The effects of intermediate distances on gene flow are equivocal. Populations SN1 and SN3 are 1300 m apart, yet they show no differentiation. In contrast, the SS populations lie 1000–1800 m distant from the SN

populations, and pairwise comparisons among these pools show significant differentiation, with Nm values from 0.39 to 0.52 (Table 3). No obvious barriers to gene flow exist between the SN and SS populations, so the reason for this difference is unknown. The Lincoln County populations are separated from the Spokane County populations by a distance of 80 km; not surprisingly, gene flow estimates between these regions are quite low.

The pattern of genetic similarity depicted in Figure 2 is consistent with Björk's (2002) designation of the Lincoln County populations of *N. leucocephala* as a separate subspecies. Unfortunately, geographic distance and subspecies identity are confounded in our sampling, so firm conclusions about genetic support for the designation are not yet warranted. For example, we have no estimate of the amount of variation that might be observed between populations within a subspecies that are separated by 80–100 km. In addition, sampling of *diffusa* populations was quite localized, even within the restricted range of the subspecies. The samples used in this study were collected before the designation of *diffusa* as a separate subspecies, and were intended to sample *N. leucocephala minima* populations separated by a range of distances. Sampling of additional populations is hampered by the fact that most vernal pools in eastern Washington occur on private land, and landowners are generally reluctant to grant access.

The genetic differentiation observed among *N. leucocephala* populations separated by relatively short distances has implications for the conservation of vernal pool habitats and their associated species. Our SS and SN populations were separated by less than 2 km, yet we detected significant genetic differentiation among them. The large number of unique haplotypes found in each population also suggests that no single pool is likely to be representative of the genetic variation found across the larger landscape. Efforts to preserve vernal pool diversity should therefore focus on protecting populations throughout the larger regions in which they occur, rather than a few localized populations with significant numbers of individuals. This pattern in genetic variation is consistent with that seen at the community level in vernal pool floras. Within the California Floristic Province over 100 species of plants are known to be endemic to, or primarily associated with, vernal pools (Holland 1976; Keeley and Zedler 1998). Despite this diversity, individual pools generally contain only 15–20 plant species, indicating a high degree of variation in species composition from pool to pool (Holland 1976; Keeley and Zedler 1998). Consequently, vernal pool conservation efforts should be undertaken over large spatial scales, so as to capture the greatest amount of biological diversity, at the population as well as the community level.

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MORPHOLOGICAL AND MOLECULAR EVIDENCE CONCERNING THE
RELATIONSHIP OF *LUPINUS POLYPHYLLUS* AND
L. WYETHII (FABACEAE)

ERICA J. WHEELER¹, RUTHANNE L. EDWARD, AND GERALDINE A. ALLEN
Department of Biology, University of Victoria, P.O. Box 3020 STN CSC,
Victoria, British Columbia V8W 3N5, Canada

ABSTRACT

Lupinus polyphyllus and *L. wyethii* are closely related members of a species complex widely distributed in western North America. Principal components analysis of morphological characters showed that these two taxa intergrade extensively, with many intermediate forms occurring. DNA sequences of the internal transcribed spacer (ITS) region in 28 individuals were variable at five base positions, both within and between taxa; some of these sequences have also been reported from related species. Molecular variation showed a geographic pattern but did not strongly reflect morphological differences. Morphological features that have been used to separate species in this group may primarily reflect local adaptation rather than underlying phylogenetic divergence. The lack of clear differentiation between these two lupines suggests that they are best treated as varieties of a single species, *L. polyphyllus*.

Key Words: *Lupinus polyphyllus*, *Lupinus wyethii*, principal components analysis, ITS, intraspecific variation.

The genus *Lupinus* (Fabaceae) comprises at least 200 species, occurring mainly in the New World (Dunn and Gillett 1966; Käss and Wink 1997a; Ainouche and Bayer 1999). *Lupinus* is especially diverse in western North America, where it includes several taxonomically difficult species complexes (Dunn and Gillett 1966; Barneby 1989; Ainouche and Bayer 1999). Members of these difficult groups exhibit plasticity in taxonomically important characters, and often appear to be separated by weak reproductive barriers, leading to abundant individuals of intermediate morphology (Dunn and Gillett 1966). Polyploidy (reported for a few species; Phillips 1957) and hybridization may also contribute to this taxonomic complexity.

One such group is centered on *Lupinus polyphyllus* Lindl. (large-leaved lupine), a widespread polymorphic species found in moist meadows throughout western North America. The taxa of the *L. polyphyllus* group intergrade extensively. Some authors (Barneby 1989; Hickman 1993) treat the *Lupinus polyphyllus* complex as a single, highly variable species; others (Dunn and Gillett 1966; Hitchcock and Cronquist 1973; Douglas et al. 1999) recognize one or more distinct species in addition to *L. polyphyllus*. Species that have been segregated from *L. polyphyllus* by various authors include *L. ammophilus* Greene, *L. burkei* S. Wats., *L. holmgrenanus* C. P. Smith, *L. prunophilus* M. E. Jones, *L. saxosus* Howell, *L. subsericeus* Robinson ex Piper, and *L. wyethii* S. Wats. One of the most detailed recent treatments of this complex is provided by Barneby (1989), who recognizes six varieties of *L. polyphyllus*, separated largely on size

characters and habitat differences: var. *ammophilus* (Greene) Barneby, var. *burkei* (Wats.) Hitchcock, var. *humicola* (A. Nels.) Barneby, var. *prunophilus* (Jones) Phillips, var. *saxosus* (Howell) Barneby, and var. *polyphyllus*. It is clear from Barneby's discussion that in addition to within-group variation, the taxa of the *L. polyphyllus* complex are connected through intermediate forms with species of several related groups, including *L. argenteus*, *L. nootkatensis*, *L. latifolius* and *L. arcticus* (Dunn and Gillett 1966; Barneby 1989).

One of the most strongly marked taxa of the *L. polyphyllus* group is *L. wyethii* Wats. (Wyeth's lupine), which occurs in steppe and montane habitats from southern British Columbia to Oregon, Montana, Wyoming and northern Nevada. *Lupinus wyethii* is known from fewer than five localities in B.C. and is considered critically imperiled, with a provincial ranking of S1 (Douglas et al. 2002). It has been variously treated as a distinct species (Douglas et al. 1999; Hitchcock and Cronquist 1973) or as the variety *L. polyphyllus* var. *humicola* (A. Nels.) Barneby (Barneby 1989). Because conservation priorities lie in protecting species that are genetically and taxonomically distinct, an understanding of the taxonomic status of *L. wyethii* is important for determining the priority it receives in conservation planning (Edward 1997).

Lupinus polyphyllus and related taxa have been included in recent molecular phylogenetic studies of *Lupinus* based on ITS and other DNA regions (Käss and Wink 1997a; Ainouche and Bayer 1999; Ree et al. 2004) and in each of these studies, *L. polyphyllus* is placed along with most other western North American lupines in a monophyletic New World clade. However, all three studies reported

¹ Author for correspondence, email: ericaw@uvic.ca

TABLE 1. MORPHOLOGICAL CHARACTERS OF *LUPINUS POLYPHYLLUS* AND *L. WYETHII* USED IN PRINCIPAL COMPONENTS ANALYSES. Means, standard deviations and ranges of variation are given for sampled specimens of each taxon.

| Characters and units of measurement | <i>Lupinus polyphyllus</i> | | <i>Lupinus wyethii</i> | |
|--|----------------------------|-----------|------------------------|----------|
| | Mean ± SD | Range | Mean ± SD | Range |
| Plant habit | | | | |
| Plant height (cm) | 55.60 ± 18.83 | 21–101.5 | 34.62 ± 8.06 | 25.5–56 |
| Stem thickness 5 cm below inflorescence (mm) | 0.32 ± 0.10 | 0.2–0.6 | 0.24 ± 0.06 | 0.1–0.3 |
| Number of lateral branches | 1.17 ± 1.31 | 0–5 | 1.83 ± 2.50 | 0–10 |
| Pubescence | | | | |
| Length of stem trichomes (mm) | 0.75 ± 0.33 | 0.3–1.5 | 0.89 ± 0.28 | 0.4–1.8 |
| Trichome density on stem (0 = none to 5 = very dense) | 2.51 ± 0.88 | 1–4 | 3.26 ± 0.54 | 2–4 |
| Trichome density on leaf upper surfaces (0 to 5) | 0.49 ± 1.00 | 0–3.5 | 3.07 ± 0.79 | 1–4 |
| Trichome density on leaf lower surfaces (0 to 5) | 2.59 ± 0.60 | 1.5–4 | 3.82 ± 0.53 | 2.5–4.5 |
| Trichome density on keel (0 to 5) | 0.60 ± 1.08 | 0–3 | 2.91 ± 0.90 | 0–4 |
| Leaves | | | | |
| Number of basal leaves | 2.55 ± 1.78 | 1–9 | 10.52 ± 11.70 | 1–40 |
| Number of cauline leaves | | | | |
| Petiole length (cm) | 8.36 ± 5.16 | 2–27 | 10.57 ± 8.19 | 2–37 |
| Number of leaflets | 15.67 ± 7.76 | 4–40.2 | 9.89 ± 2.99 | 4.6–18.5 |
| Length of middle leaflet (cm) | 10.2 ± 2.7 | 6–15 | 9.0 ± 1.1 | 7–11 |
| Length/width ratio of middle leaflet | 5.87 ± 1.78 | 2.5–10.8 | 3.75 ± 1.41 | 2.1–7.6 |
| Shape of leaflet tip (1 = acute, 2 = rounded to mucronate, 3 = obtuse) | 5.73 ± 1.76 | 3–10.8 | 7.61 ± 2.52 | 2.7–14.3 |
| | 2.40 ± 0.79 | 1–3 | 2.98 ± 0.10 | 2.5–3 |
| Inflorescence | | | | |
| Number of racemes | 1.17 ± 0.56 | 1–4 | 2.17 ± 1.67 | 1–7 |
| Number of flowers in terminal raceme | 54.07 ± 26.93 | 12–118 | 31.29 ± 9.29 | 15–52 |
| Length of terminal raceme (cm) | 16.04 ± 6.94 | 3.8–34.3 | 9.73 ± 4.01 | 4.2–19.8 |
| Pedicle length (mm) | 0.66 ± 0.23 | 0.2–1.2 | 0.57 ± 0.15 | 0.3–0.9 |
| Flowers (measurement from lowermost open flower) | | | | |
| Banner length (mm) | 1.08 ± 0.16 | 0.7–1.4 | 1.02 ± 0.15 | 0.7–1.3 |
| Keel length (mm) | 1.46 ± 0.22 | 0.8–2 | 1.35 ± 0.17 | 1.0–1.6 |
| Ratio of upper and lower calyx lobe lengths | 0.85 ± 0.13 | 0.57–1.13 | 0.88 ± 0.10 | 0.69–1 |

largely unresolved relationships within this group. Ree et al. (2004), in phylogenetic analyses based on ITS and two paralogous LEGCYC genes, found that two accessions of *L. polyphyllus* were interspersed with the related species *L. andersonii*, *L. sericeus* and *L. argenteus*. The findings of these authors suggest that the western lupines are recently diverged in comparison with other lupine groups, and may also imply ongoing hybridization and reticulate evolution.

In this paper, we present morphological and molecular evidence concerning the taxonomic relationship of *L. polyphyllus* and *L. wyethii*. We used (1) multivariate analyses of morphological characters from herbarium specimens to assess the divergence of these taxa and the usefulness of various traits for distinguishing them, and (2) sequence variation in the internal transcribed spacer (ITS) region of the nuclear ribosomal RNA gene to assess differences between the two taxa, intraspecific variation, and the geographic distribution of genetic variants. We also assessed the relationship of these two taxa to other western North American lupines by comparing our data to the published ITS1 and ITS2 sequences available for this group.

METHODS

Morphological Analyses

For analysis of morphological variation, specimens of both taxa were obtained from the following herbaria: OSC, UBC, UVIC, V, and WTU. We included specimens from British Columbia, Washington, Oregon, Idaho, and Montana. Although most of the accessions of *L. polyphyllus* used in this study were not identified to subspecies or variety, they represented a large range of morphological variation within the species.

We compiled an initial list of 75 morphological characters (see Edward 1997 for complete list), including all those that have been used to distinguish *L. polyphyllus* and *L. wyethii*. From these we selected 22 characters, including the characters used to separate the two taxa, for the final analyses (Table 1). We included characters that (i) represented all parts of the plant, (ii) were obtainable from all specimens, (iii) could be determined repeatably, (iv) did not require destructive sampling, and (v) were not highly correlated with other characters ($r < 0.9$). When multiple measurements of a character were made from a specimen, these were averaged

TABLE 2. *LUPINUS* SPECIMENS USED FOR DNA ANALYSIS.

| Species | Location and collector | Herbarium | GenBank # |
|-----------------------|---|-----------|-----------|
| <i>L. polyphyllus</i> | Alaska, Mt. Marathon, J.A. Calder 6207 | V | AY948993 |
| <i>L. polyphyllus</i> | British Columbia, Cronin Mt., G. Mendel 83 | V | AY948994 |
| <i>L. polyphyllus</i> | British Columbia, Copper City, G. Mendel 85 | V | AY948995 |
| <i>L. polyphyllus</i> | British Columbia, Liard Hot Springs, T.C. Brayshaw s.n. | V | AY949017 |
| <i>L. polyphyllus</i> | British Columbia, Cottonwood River, T.C. Brayshaw s.n. | V | AY948996 |
| <i>L. polyphyllus</i> | British Columbia, Summit Lake, R. Long 2-4-71 | V | AY949018 |
| <i>L. polyphyllus</i> | British Columbia, Ashnola Provincial Forest, T.C. Brayshaw 77-531 | V | AY949010 |
| <i>L. polyphyllus</i> | British Columbia, Mayne Island, H. Janszen 1094 | V | AY948997 |
| <i>L. polyphyllus</i> | British Columbia, Port Alberni, W. Van Dieren 353 | V | AY948998 |
| <i>L. polyphyllus</i> | Washington, Olympic National Park, W. Van Dieren 518 | V | AY949011 |
| <i>L. polyphyllus</i> | British Columbia, Dewdney Island, R.T. Ogilvie 8471110 | V | AY948999 |
| <i>L. polyphyllus</i> | British Columbia, Shawnigan Lake, B. Turner 1486 | UVIC | AY949000 |
| <i>L. polyphyllus</i> | British Columbia, Cowichan River, B. Chapman 853 | UVIC | AY949012 |
| <i>L. polyphyllus</i> | British Columbia, Nanaimo River, W. Fleming M-4 | UVIC | AY949013 |
| <i>L. polyphyllus</i> | Oregon, Polk Co., R. Halse 2844 | UVIC | AY949001 |
| <i>L. polyphyllus</i> | British Columbia, Manning Provincial Park, G. Rushton s.n. | UVIC | AY949019 |
| <i>L. polyphyllus</i> | British Columbia, Quesnel, C. Selzler 11 | UVIC | AY949002 |
| <i>L. polyphyllus</i> | Washington, Chelan Co., M. Denton 3722 | WTU | AY949020 |
| <i>L. polyphyllus</i> | Idaho, Camas Co., J.H. Christ 53-27 | WTU | AY949005 |
| <i>L. polyphyllus</i> | Washington, Wallowa-Whitman National Forest, B. Bafus 365 | WTU | AY949006 |
| <i>L. polyphyllus</i> | Washington, Lewis Co., S. Gage 29 | WTU | AY949003 |
| <i>L. polyphyllus</i> | Washington, Clark Co., R. Halse 3872 | WTU | AY949004 |
| <i>L. wyethii</i> | British Columbia, Keremeos, T.C. Brayshaw 77-1011 | V | AY949014 |
| <i>L. wyethii</i> | Alberta, Kananaskis Valley, R.T. Ogilvie 9862 | V | AY949007 |
| <i>L. wyethii</i> | Washington, Vernita, S. Mitchell s.n. | UVIC | AY949008 |
| <i>L. wyethii</i> | British Columbia, Vernon, S. Mitchell 481 | UVIC | AY949015 |
| <i>L. wyethii</i> | Wyoming, Teton Co., C.L. Porter 9325 | WTU | AY949009 |
| <i>L. wyethii</i> | Utah, Duchesne Co., A. Cronquist 11387 | WTU | AY949016 |

to give a single value of each character for that specimen. We used a total of 70 herbarium specimens (47 of *L. polyphyllus* and 23 of *L. wyethii*) for multivariate analysis, sampling only well-preserved specimens from which all morphological measurements could be obtained.

Principal components analysis (PCA) of the standardized data was carried out using Statistix for Windows (Analytical Software, Tallahassee, FL). We examined correlations of the first and second principal component (PCA-1 and PCA-2) scores with all morphological characters to determine which characters contributed most to the observed patterns. We also examined correlations of PCA scores and individual morphological characters with latitude, longitude and elevation.

Molecular Analyses

Leaf material was taken, with permission, from herbarium collections at UVIC, V and WTU (Table 2). We selected multiple-leaved specimens that could be sampled with minimum loss of morphological information. Total DNA was isolated using a modified CTAB extraction protocol (Doyle and Doyle 1990; Wheeler 2000). Because we carried out the two phases of this study separately and used different specimen selection criteria, the morphological and molecular analyses were based for the most part on different sets of specimens.

The entire ITS region including the 5.8S gene

was amplified by PCR using primers 1406F and 307R (Soltis and Kuzoff 1995). Amplification was carried out in 100 µL reactions, including 1µg genomic DNA, 10% 10× amplification buffer, 0.2 mM dNTPs, 0.25 µM of each primer, 2 units Taq DNA polymerase (GibcoBRL, Burlington, Canada) and 5% DMSO. Amplification reactions were performed on an MJ Research PTC-200 DNA Engine Thermal Cycler as follows: 94°C for 3 min, 30 cycles of 94°C for 30 sec, 55°C for 60 sec and 72°C for 60 sec, and final extension at 72°C for 10 min. PCR products were purified with a QIAquick PCR purification kit, and were then sequenced directly. A DNA Sequencing Ready Reaction Kit (ABI) was used for cycle sequencing reactions, with the two amplification primers and the primer ITS4 (White et al. 1990). DNA sequencing was carried out on an ABI Prism 377 DNA automated sequencer.

ITS sequences were aligned using ClustalX v. 1.8 (Thompson et al. 1997). The limits of the ITS region were determined by comparison with published *L. polyphyllus* sequences deposited in GenBank (Ainouche and Bayer 1999; Käss and Wink 1997a). GenBank accession numbers for sequences reported here are given in Table 2. We compared our results with all published ITS1 and ITS2 sequences for western North American lupines (excluding the 5.8S gene, which was not available for all accessions) to assess the taxonomic and geographic distribution of sequences in this group.

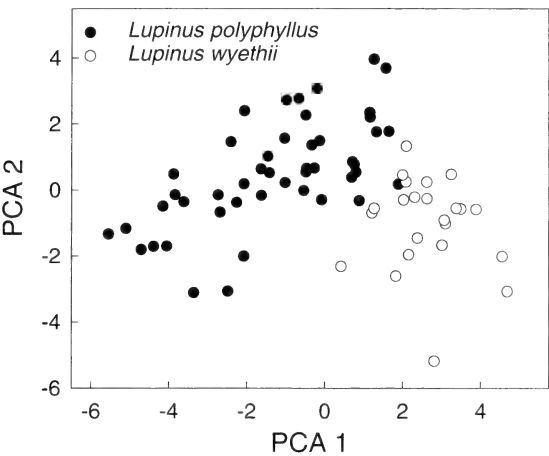


FIG. 1. Principal components of morphological variation in *Lupinus polyphyllus* and *L. wyethii*. Analysis is based on 22 characters and 70 specimens.

RESULTS

Morphological Variation

Principal components analysis (Fig. 1) indicated that *L. polyphyllus* and *L. wyethii* differ morphologically. However, the two taxa clearly form a complete morphological continuum, with many intermediate specimens. Correlations of various characters with principal component scores, particularly along the first axis, reflected the morphological differences between the two taxa. Eleven characters were significantly correlated ($P < 0.05$) with one or both axes (Table 3). Axis 1 scores were positively correlated with trichome density of leaf upper surface and keel, number of basal leaves, and number of racemes; and negatively correlated with several size-related traits including height, leaf characters (petiole and leaflet lengths), and inflorescence characters (length, flower number). Axis 2 scores were negatively correlated with leaf number (both basal and cauline), number of lateral branches, and leaf upper surface trichome density.

Morphological variation in *L. polyphyllus* and *L. wyethii* is summarized for all characters in Table 1. The two taxa differed mainly in pubescence and size. *Lupinus wyethii* was usually more densely pubescent, particularly on leaf upper surfaces (a diagnostic character) and on the keel. It was also generally of shorter stature than typical *L. polyphyllus*, with smaller and often more numerous leaves, a greater tendency toward branching, and shorter, fewer-flowered inflorescences. However, all characters showed at least some overlap, and many were highly variable within each taxon. Pubescence of leaf upper surfaces is considered the diagnostic character for separating these two species. *Lupinus polyphyllus* (characterized as glabrous on leaf upper surfaces) was at least somewhat pubescent on basal and/or cauline leaf upper surfaces in 11 out of 47 plants examined; *L. wyethii* (characterized as pubescent on upper leaf surfaces) was pubescent on leaf upper surfaces in all 23 specimens, but sometimes only sparsely so. Keel pubescence, another diagnostically useful character, was present in all but one of the 23 *L. wyethii* specimens, but lacking in only 38 of the 47 *L. polyphyllus* specimens. Overlap was generally much greater in other morphological characters, and within-plant variation in some traits also suggested that these lupines are phenotypically plastic. Virtually all characters measured in this study showed continuous variation.

Morphology also varied with geographic location and elevation. Latitude of the sampled specimens was positively correlated with PCA-2 score ($r = 0.261$), and longitude was negatively correlated with PCA-1 score ($r = -0.561$). Both latitude and longitude were also significantly correlated with many individual morphological characters. These results reflect in part the different distributions of these taxa, *L. polyphyllus* generally occurring further north and west than *L. wyethii* (Fig. 2a). Elevation showed a significant positive correlation with both principal component axes ($r = 0.610$ with PCA-1; $r = 0.245$ with PCA-2) as well as with many morphological characters, indicating that typ-

TABLE 3. PEARSON CORRELATIONS OF MORPHOLOGICAL CHARACTERS WITH FIRST AND SECOND AXIS PCA SCORES. Only characters with significant correlation coefficients ($P < 0.05$) are included.

| Morphological characters | Correlation coefficients | |
|---|--------------------------|--------|
| | PCA 1 | PCA 2 |
| Plant height | -0.315 | |
| Number of lateral branches | | -0.304 |
| Trichome density on upper leaf surfaces | 0.388 | -0.425 |
| Trichome density on keel | 0.481 | |
| Number of basal leaves | 0.446 | -0.267 |
| Number of cauline leaves | | -0.272 |
| Petiole length | -0.336 | |
| Length of middle leaflets | -0.265 | |
| Number of racemes | 0.316 | |
| Number of flowers in terminal raceme | -0.379 | |
| Length of terminal raceme | -0.360 | |

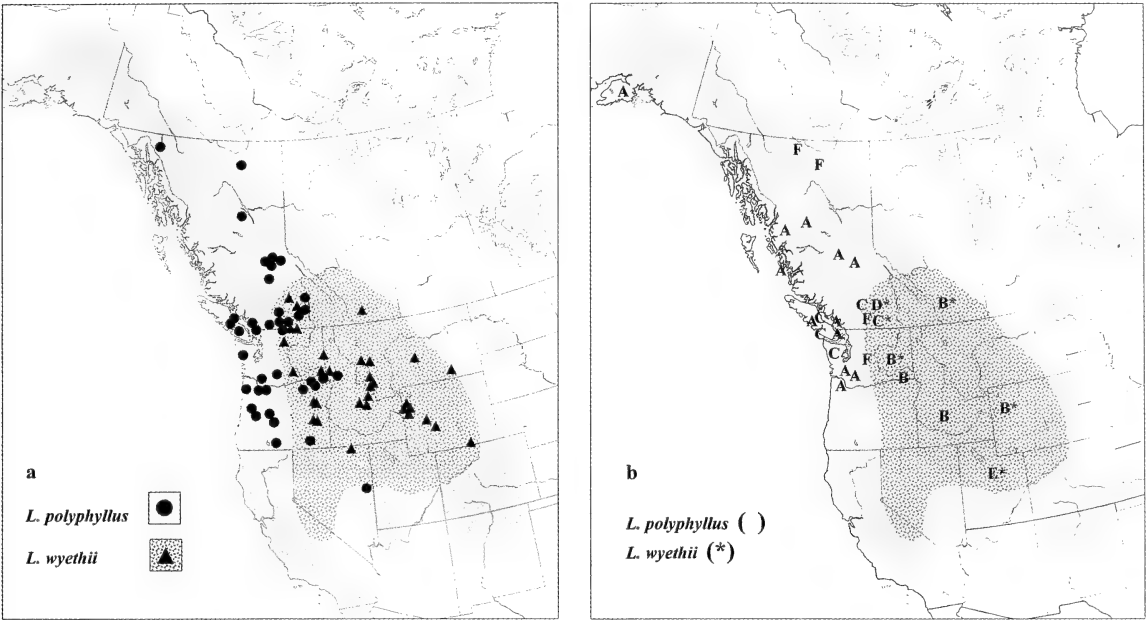


FIG. 2. Ranges of *Lupinus polyphyllus* and *L. wyethii*, with geographic distributions of morphological and molecular forms. (a) Specimens used for PCA of morphological variation, (b) Sequence variants for ITS found in the two taxa (See Table 4).

ical *L. wyethii* tended to be more commonly found at high elevations

Molecular Variation

The length of the ITS region (including the 5.8S gene) was 628 base pairs in all 28 *Lupinus* specimens examined, with no insertions, deletions or inversions. Sequence chromatograms showed no evidence of mixed sequences within individuals. Five variable base positions were found, each characterized by a single nucleotide polymorphism; three of these occurred in the ITS1 region, and one each in the 5.8S gene and the ITS2 region. This variation yielded six different sequences (variants A to F, Table 4), each differing from the others by a single nucleotide substitution. The most common variant (A) was found in 12 of the 28 plants sampled, and

the least common (D and E) were each found in only one individual.

ITS sequences showed some differences between the two taxa (Table 4), but some overlap. Of the six sequence variants found, two (A and F) were exclusive to *L. polyphyllus*, and two (D and E) to *L. wyethii*; the remaining two (B and C) occurred in both taxa. The shared variants were found in 27% of the *L. polyphyllus* specimens and 67% of the *L. wyethii* specimens (Table 4). Within *L. polyphyllus* there was no correspondence between morphological variety and ITS sequence.

The ITS sequence variants showed striking differences in their geographic distribution (Fig. 2b). Variant A, the most common *L. polyphyllus* variant, occurred from coastal Alaska through western B.C. and Washington to northwestern Oregon, well north

TABLE 4. SEQUENCE VARIANTS OF THE INTERNAL TRANSCRIBED SPACER (ITS) REGION IN *L. POLYPHYLLUS* AND *L. WYETHII*, SHOWING BASE POSITION OF NUCLEOTIDE POLYMORPHISMS AND NUMBER OF SPECIMENS IN WHICH EACH VARIANT WAS FOUND.

| Sequence variant | Polymorphic base positions in aligned ITS sequence | | | | | Number of specimens showing variant | |
|------------------|--|-----|-----|-----|-----|-------------------------------------|-------------------|
| | 116 | 166 | 197 | 373 | 412 | <i>L. polyphyllus</i> | <i>L. wyethii</i> |
| A | T | G | G | C | C | 12 | 0 |
| B | C | G | G | C | C | 2 | 3 |
| C | T | T | G | C | C | 4 | 1 |
| D | T | G | A | C | C | 0 | 1 |
| E | T | G | G | T | C | 0 | 1 |
| F | T | G | G | C | T | 4 | 0 |

and west of the geographic range of *L. wyethii*. Variant F was also widely distributed, but occurred further east in more continental climates. Variant B, occurring to the south and east, and variant C, of northwestern Washington and southern B.C., occurred in both *L. polyphyllus* and *L. wyethii* where the ranges of the two species overlap. Much of the geographic range that we examined was characterized by particular sequence variants, indicating considerable genetic structure within the two taxa.

Of the six ITS sequence variants we found (Table 4), two (*L. wyethii* sequences D and E) were novel, one (*L. polyphyllus* sequence C) was previously reported from *L. polyphyllus*, and three have been reported from other species (Ainouche and Bayer 1999; Ree et al. 2004). Sequence A from *L. polyphyllus* has also been found in *L. argenteus*, *L. aridus*, and *L. rivularis*. Sequence B, found in both *L. polyphyllus* and *L. wyethii*, is identical to sequences reported from *L. andersonii*, *L. argenteus*, *L. leucophyllus*, *L. sericeus* and *L. sulphureus*. Sequence F from *L. polyphyllus* is identical to sequences reported from *L. arcticus* and *L. breweri* var. *bryoides*. Ree et al. (2004) and Käss and Wink (1997a) found sequence variants for *L. polyphyllus* different from those reported here; altogether, seven ITS variants are known from *L. polyphyllus*.

DISCUSSION

Lupinus polyphyllus and *L. wyethii* are not well differentiated morphologically, as indicated by the range of morphological intermediates found in this study, and the absence of any clear morphological discontinuity separating them (Fig. 1, Table 1). These two taxa have very similar floral features, and are separated only by quantitative differences in size and pubescence of vegetative structures. Such vegetative differences may indicate adaptation of genotypes to local habitats, but may also reflect phenotypic plasticity, a possibility supported by our observations that characters sometimes showed within-plant variation. In either case, caution should be used in giving such differences formal taxonomic recognition.

Lupinus polyphyllus and *L. wyethii* were both variable for ITS, each possessing four of the six sequence variants found. Two variants were present in both taxa. All sequence variants differed by only one base substitution, thus the molecular differences between *L. polyphyllus* and *L. wyethii* were no greater in magnitude than the differences among individuals within *L. polyphyllus* or *L. wyethii*. Comparison of all available ITS sequences for western North American *Lupinus* species (Käss and Wink 1997a; Ainouche and Bayer 1999; Ree et al. 2004) revealed a similar pattern; intraspecific sequence differences exist in all of the other eight species (*L. arboreus*, *L. arcticus*, *L. argenteus*, *L. latifolius*, *L. lepidus*, *L. rivularis*, *L. sericeus*, and *L. succulentus*) for which multiple ITS sequences

are available and these sequences were commonly shared by different taxonomic species. The relatively high level of intraspecific variation that we found in *L. polyphyllus* may therefore occur throughout this group.

The ITS sequences available for other western North American lupines also indicated a lack of divergence between recognized species within this group. In their phylogenetic study of *Lupinus* based on ITS, Ainouche and Bayer (1999) identified an apparently monophyletic western North American clade of about 30 species (clade E), supported by a single base-pair insertion in ITS1. This clade was poorly differentiated into subclades, and showed the least sequence divergence of all *Lupinus* lineages. Käss and Wink (1997a) reported a similar lack of divergence in ITS sequences of this group, showing identical ITS sequences in *L. polyphyllus* and several other western species including *L. arboreus*, *L. arcticus*, *L. nootkatensis* and *L. perennis*. The additional ITS sequences reported here for *L. polyphyllus* are identical to sequences reported by Käss and Wink (1997a), Ainouche and Bayer (1999), and Ree et al. (2004) for other species, including *L. argenteus*, *L. sulphureus*, *L. leucophyllus*, *L. andersonii*, *L. breweri* var. *bryoides* and *L. sericeus*. ITS sequences are present in multiple copies in an individual genome and undergo concerted evolution, which can present problems for inferring phylogenetic relationships (Alvarez and Wendel 2003). Irrespective of these problems, however, the occurrence of the same ITS variant in different taxonomic species suggests close relationships among these species. Such a pattern could reflect reticulate relationships resulting from hybridization (perhaps involving polyploidy), or simply recent origins and incomplete divergence of taxa.

In this study, we observed distinct geographic distributions of molecular variants, with both east-west and north-south differences. Other authors (Allen et al. 1996; Soltis et al. 1997; Tremblay and Schoen 1999; Golden and Bain 2000; Dobes et al. 2004) have identified similar patterns of intraspecific molecular variation in other western North American species groups, often reflecting the consequences of recolonization after Pleistocene deglaciation. A striking result of our study was that *L. polyphyllus* and *L. wyethii* accessions from the same geographic region often yielded the same ITS sequence (Fig. 2b), suggesting that few genetic barriers separate the two taxa. Although sampling intensity was low, many ITS variants from other species were also geographically localized.

In summary, the amount of molecular divergence among western North American lupines is low in comparison with other lupine clades, and morphological characters commonly used to distinguish species generally do not coincide with patterns of molecular variation. As other authors have also concluded (Ainouche and Bayer 1999; Ree et al. 2004), this suggests that western North American

lupines are a recently originated group. Many of the morphological species currently recognized in this group appear not to be genetically distinct, and may even be polyphyletic. The available data for these species suggest that there is little basis for subdividing western lupines too finely on the basis of morphological differences. Although *L. wyethii* is one of the most recognizable segregates of *L. polyphyllus*, the morphological and molecular evidence together suggest that it is best treated as *L. polyphyllus* var. *humicola*.

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CLIMATIC ASSESSMENT OF A 580-YEAR *CHAMAECYPARIS LAWSONIANA* (PORT ORFORD CEDAR) TREE-RING CHRONOLOGY IN THE SISKIYOU MOUNTAINS, USA

ALLYSON L. CARROLL AND ERIK S. JULES¹

Department of Biological Sciences, Humboldt State University, Arcata, CA 95521

ABSTRACT

Tree-ring data from *Chamaecyparis lawsoniana* (A. Murr.) Parl. (Port Orford cedar; Cupressaceae) were used to create a standardized chronology, assess the local, limiting factors on radial growth, and investigate the extent of a unique climatic event. We produced a 580-year tree-ring chronology (A.D. 1420 to 2000) from a large number of cedars ($n = 1537$) sampled in one 37 km² area in the Siskiyou Mountains of southwestern Oregon and northern California. This chronology represents an area with few long-term climatic studies and a species with no dendrochronological data. We found radial growth to be positively correlated with year-round soil moisture conditions, specifically with cool, wet conditions in summer and warm, wet conditions in winter. The year 1739 stood out as a climatic pointer year with the smallest ring width index for the entire chronology and anatomically distinctive damage to the latewood of 1738 and earlywood of 1739. This pointer year was consistently identified across watersheds, topographic position (e.g., streamside, hillslope), and the range of the cedar, corresponding to an extreme, single-year drought occurring throughout the Pacific Northwest.

Key Words: *Chamaecyparis lawsoniana*, Port Orford cedar, Siskiyou Mountains, tree-ring analysis, 1739, drought.

Tree-ring records have long been accepted as an effective proxy method to examine paleoclimatic conditions (Douglass 1920). Because the width of annual growth rings varies with the surrounding climatic conditions (e.g., temperature and precipitation), a temporal record of past climatic variability is established showing trends as well as specific events (e.g., severe single-year droughts). Tree-ring chronologies can indicate limiting growth factors for a particular species (i.e., the principle of sensitivity), provide insight into long-term climatic conditions, and identify the basic biology (e.g., physiology, autecology) of particular tree species (Fritts 1976).

This study focused on the tree-ring record of *Chamaecyparis lawsoniana* (A. Murr.) Parl. (Port Orford cedar; Cupressaceae), a conifer endemic to southwestern Oregon and northern California (Fig. 1). The chronology presented here represents cedars located in the Siskiyou Mountains, a region containing one of the most diverse conifer forests in the world (Whittaker 1960). Our chronology establishes important baseline climatic information given the paucity of long-term climatic data for this region and the absence of Port Orford cedar tree-ring chronologies.

The ecology and conservation of Port Orford cedar has become an increasingly important topic as additional portions of the cedar's range continue to be infected by a fatal, non-native root pathogen,

Phytophthora lateralis. The source pathogen, first detected in the cedar's range in 1952, spreads downstream in flowing water and also along road systems when spores are dispersed from mud on vehicles. Because Port Orford cedar is a commercially valuable conifer and a dominant species in many parts of its range, its continued loss has caused significant economic and ecological impacts to the Pacific Northwest (Hansen et al. 2000). As part of an earlier study, we and our colleagues (Jules et al. 2002) assessed the spread dynamics of this pathogen by using dendrochronological techniques as a tool to reconstruct the infection history of cedars, resulting in tree-ring data from 1537 cedars.

The large dataset resulting from this previous study yielded strong correlations among trees and a record covering a long time span (A.D. 1361 to present). Thus, the tree-ring data allowed for the establishment of a standardized chronology and assessment of Port Orford cedar's radial growth patterns compared to corresponding climatic data. For example, many of the tree cores showed physical damage occurring after the latewood of 1738 and during the springwood of 1739, indicating an extreme, single-year event (Fig. 2). This damage coincided with the year 1739 being the smallest growth ring of the entire 580-year chronology.

To summarize, our objectives were to: 1) develop a standardized chronology for Port Orford cedar in the Siskiyou Mountains 2) determine which climatic factors the radial growth patterns best represent and 3) investigate the occurrence of the unique climatic event.

¹ Author for correspondence, email: erik.jules@humboldt.edu.

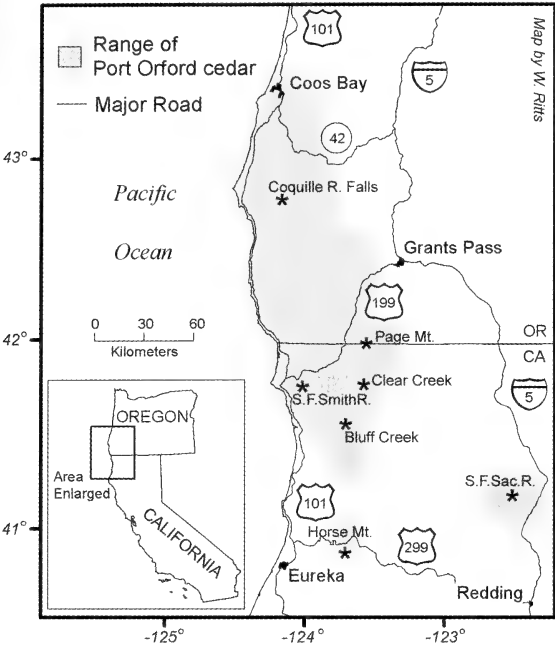


FIG. 1. Approximate range of Port Orford cedar and locations of sites where increment cores were sampled. See Table 1 for details.

METHODS

Study Organism and Study Area

The geographic range of Port Orford cedar extends from the northern end of the California Coast Ranges to the uplifted marine terraces and Coast Ranges near Coos Bay, Oregon, and inland along the drainages of the Klamath and Siskiyou Mountains (Zobel et al. 1985; Fig. 1). This region has cool, wet winters and warm, dry summers that limit the cedar to areas that maintain significant soil moisture year-round (Zobel and Hawk 1980). Accordingly, over much of its range, the cedar is re-

stricted to riparian areas, wetlands, and mesic uplands.

Our study area for the chronology includes 37 km² near Page Mountain situated on the Oregon/California border and within the Siskiyou National Forest. We sampled individual cedars from five watersheds within the study area: Little Elder Creek, Elder Creek, Page Creek, Dunn Creek, and Poker Creek. For many trees sampled, the topographic position of the cedar was recorded as one of six types (active channel, streambank, floodplain, high floodplain, terrace, or hillslope). Trees within ~20 m of the streams were sampled, accounting for ~80 to 95% of the cedar's population at our study site. This sampling was random with regards to age, size, and height of trees (Kauffman 2003).

Tree-Ring Data and Chronology

In the Page Mtn. study area, 3350 cores from 1537 cedars were sampled and crossdated. All the cores in this study were sampled using increment borers and prepared using standard dendrochronological methods (Stokes and Smiley 1968). We used a combination of visual techniques and the software COFECHA for crossdating (Holmes 1983). Cores were measured to 0.001 mm precision using a Velmex measuring system. Only series with strong correlations were added to the original, master chronology that had a total of 965 series from 593 cedars.

The software ARSTAN was used to standardize the chronology (Cook 1985). The ARSTAN standardization process removed the non-climatic growth trend from each series and collapsed all the series into a single numeric representation of the tree-ring pattern based around an index of 1.0. For the standardized ARSTAN chronology, 65 series from 61 cedars were chosen based on the criteria of high COFECHA correlation coefficients, long time span coverage, and simple detrending options (negative exponential curve, linear regression, or

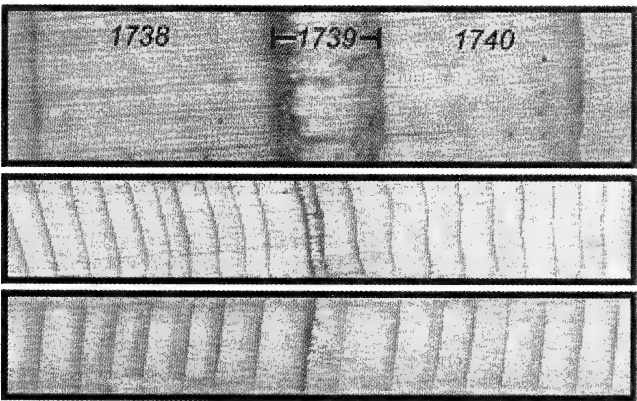


FIG. 2. Examples of the anatomical damage to the latewood 1738 and earlywood 1739 found in Port Orford cedar tree cores. Contact authors for higher resolution image.

TABLE 1. LOCATION AND CORRESPONDING SAMPLE SIZE OF INDIVIDUAL CEDARS FOR ALL STUDY SITES.

| Site | Latitude (°N) | Longitude (°W) | Number of cedars sampled |
|-----------------------------|---------------|----------------|--------------------------|
| Page Mountain | 42.00 | 123.34 | 271 |
| Coquille River Falls | 42.43 | 124.02 | 13 |
| South Fork Smith River | 41.46 | 124.00 | 4 |
| Bluff Creek at Fish Lake | 41.16 | 123.41 | 5 |
| Clear Creek | 41.45 | 123.38 | 13 |
| South Fork Sacramento River | 41.15 | 122.26 | 16 |
| Horse Mountain | 40.50 | 123.44 | 3 |

horizontal line through the mean). We selected the conservative approaches of single detrending and the standard (STD) version of the ARSTAN generated chronology for our analyses.

Climate Data

Historical monthly records from A.D. 1895 to 2000 for temperature, precipitation, and Palmer Drought Severity Index (PDSI) were obtained from the U.S. National Climatic Data Center (NCDC). The PDSI reflects long-term soil moisture availability and incorporates the effects of temperature, precipitation, and evapotranspiration (Palmer 1965). For each climatic factor, we chose Oregon Climate Division 3 because it best captures the conditions of our study site and uses measurements from several stations in southwestern Oregon. Regional data from several weather stations reduce local anomalies from single stations and often provide more reliable data than single stations for the investigation of tree-ring chronologies (Blasing et al. 1981).

Pearson correlation coefficients were used to assess climatic influences on radial growth. While evaluating such correlations, it is important to consider that climatic conditions in the previous year(s) may affect the growth of the current year's ring (Fritts 1976). Thus, although the growing season of Port Orford cedar is approximately from April to September, the conditions from November of year ($t - 2$) to the current September (year t) were also considered. In addition, correlations were calculated between the ring width index and the cumulative average of the climatic factors from the previous September to the current September to allow for an assessment of conditions on an annual scale. The software program NCSS 2001 was used for all correlation tests (Hintze 2001).

Extreme Event Indicators

For each cedar that was old enough to capture the 1739 growth ring, the presence or absence of physical damage was recorded and the growth index was calculated. Physical damage was evident in the form of abnormal cell structure, discoloration, and often resin formation to the latewood of 1738 and earlywood of 1739. The growth index

was defined as the ratio of the width of the 1739 ring to the average width of the five rings before and after 1739. This index allowed for a size comparison of a particular year with the surrounding years experiencing similar longer-term conditions. A similar technique was recently developed by Knapp et al. (2002) and called a climatic pointer year index. To assess whether the growth index differed between geomorphologic positions, we used a Kruskal-Wallis test. To test whether physical damage was found more frequently on some geomorphologies, we used a chi-square analysis.

Regional Sampling

To investigate the spatial extent of the 1739 extreme climatic event, we sampled cedars at six sites across its range in addition to Page Mtn. (Table 1, Fig. 1). Regional site selection was principally dictated by finding areas that were accessible and sufficiently old to include the 1739 growth ring. Since most of the northern extent of the cedar's range is on private land, these areas were difficult to access and also had few old trees, resulting in limited sampling there. Sampling at the regional sites was less intensive than the sampling at the Page Mtn. site since we were only sampling large individuals that show the 1739 year. Evidence of the extreme event would indicate it affected the area; however, given the smaller sample sizes, absence of the indicators would not preclude that the event affected the area.

RESULTS

Chronology

The overall COFECHA series correlation for the initial 965 series in the master chronology was $r = 0.509$ (critical $r = 0.328$ where $P \leq 0.01$). The best 65 of these series were used to develop the ARSTAN standardized chronology. The Expressed Population Signal (EPS) for the ARSTAN chronology was 0.94, where a value of 0.85 is generally regarded as the level of acceptable confidence (Wigley et al. 1984; Briffa 1995). EPS gauges the quality of the mean chronology and is dependent upon the mean correlation coefficient (RBAR) of the series and the sample size. The RBAR had a value of 0.198. The standardized chronology spans

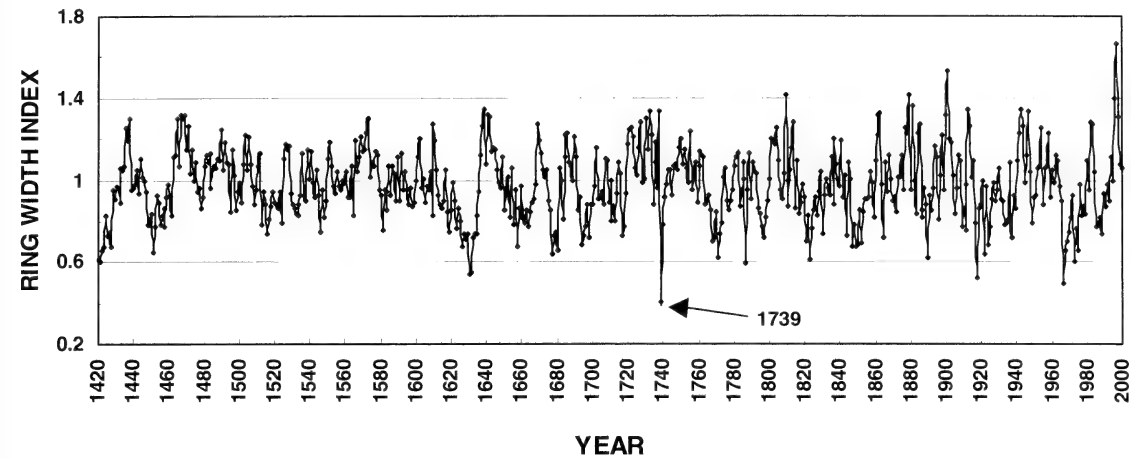


FIG. 3. Port Orford cedar standardized tree-ring chronology from A.D. 1420 to 2000 for the Page Mtn. study area in the Siskiyou Mountains of southwestern Oregon and northern California. The chronology is standardized around the mean index of 1.0. The year 1739 is indicated.

580 years of radial growth (A.D. 1420 to 2000) (Fig. 3). This dataset can be accessed via the International Tree-Ring Data Bank (ITRDB) at <<http://www.ngdc.noaa.gov/paleo/treering.html>> under the site name Page Mountain.

Climate/Growth Relationships

Tree-ring growth was negatively and significantly correlated with temperature of June ($r = -0.428$, $P < 0.001$), July ($r = -0.204$, $P = 0.037$), and the previous June ($r = -0.249$, $P = 0.011$; Fig. 4A). Growth was positively and significantly correlated with the temperature for the previous December ($r = 0.233$, $P = 0.017$) and the December before that ($r = 0.192$, $P = 0.051$). Precipitation for the current June ($r = 0.330$, $P < 0.001$) and previous December ($r = 0.272$, $P = 0.005$) show significant, positive correlations with ring width (Fig. 4C). Precipitation for the current May ($r = 0.162$, $P = 0.097$), previous May ($r = 0.278$, $P = 0.004$), and previous June ($r = 0.164$, $P = 0.095$) show positive correlations with the growth index. The Pearson tests showed significant, positive correlations between radial growth and PDSI for all months from the current September through the previous February (Fig. 4E). The strongest correlations were for the current June ($r = 0.421$, $P < 0.001$) and July ($r = 0.425$, $P < 0.001$).

Considering that the months of the current June and the previous December both have strong correlations for temperature and precipitation, we calculated the Pearson correlations between these months to test for possible autocorrelation of conditions among these summer and winter months. Neither precipitation ($r = 0.123$, $P = 0.212$) nor temperature ($r = 0.151$, $P = 0.125$) showed a significant relationship between June and December. Likewise, exploration of possible correlations between conditions of months of concern in sequen-

tial years did not show significant correlations for either temperature or precipitation. The correlations for annual conditions revealed significant relationships for PDSI ($r = 0.418$, $P < 0.001$) and precipitation ($r = 0.300$, $P = 0.002$) but not for temperature ($r = -0.007$, $P = 0.943$).

1739 Extreme Event

The year 1739 represented the lowest ring width index of the entire 580-year Port Orford cedar chronology at the Page Mtn. study site (Fig. 3). For this standardized chronology, the year 1739 had a ring width index of 0.408 in relation to the mean index of 1.0 ($SD = 0.358$). This low index value coincides with the striking visually distinctive damage that occurs on many cores after the latewood of 1738 and into the springwood of 1739 (Fig. 2).

In the entire Page Mtn. study site, 53.5% of the 271 cedars old enough to capture the 1738/1739 rings showed physical damage and the average growth index of 1739 was 0.601 (Table 2). Although sample sizes were too small in one watershed to perform statistical comparisons among watersheds, the growth index for 1739 was consistently below average for all watersheds and physical damage was evident in all watersheds with a range of 34.1 to 100% of cedars showing damage (Table 2). Physical damage to the 1738/1739 rings occurred in cedars across all geomorphologies (range 47.1–63.6%) and the proportion of trees exhibiting damage did not differ significantly between geomorphic categories ($\chi^2 = 1.96$, $df = 5$, $P = 0.853$). The growth index was consistently below average with a range of 0.519 to 0.615 in all geomorphic categories. There were no significant differences in growth index between geomorphic categories ($H = 3.56$, $df = 5$, $P = 0.614$).

Cedars at all regional sites, except for Horse Mtn., showed physical damage to the 1738/1739

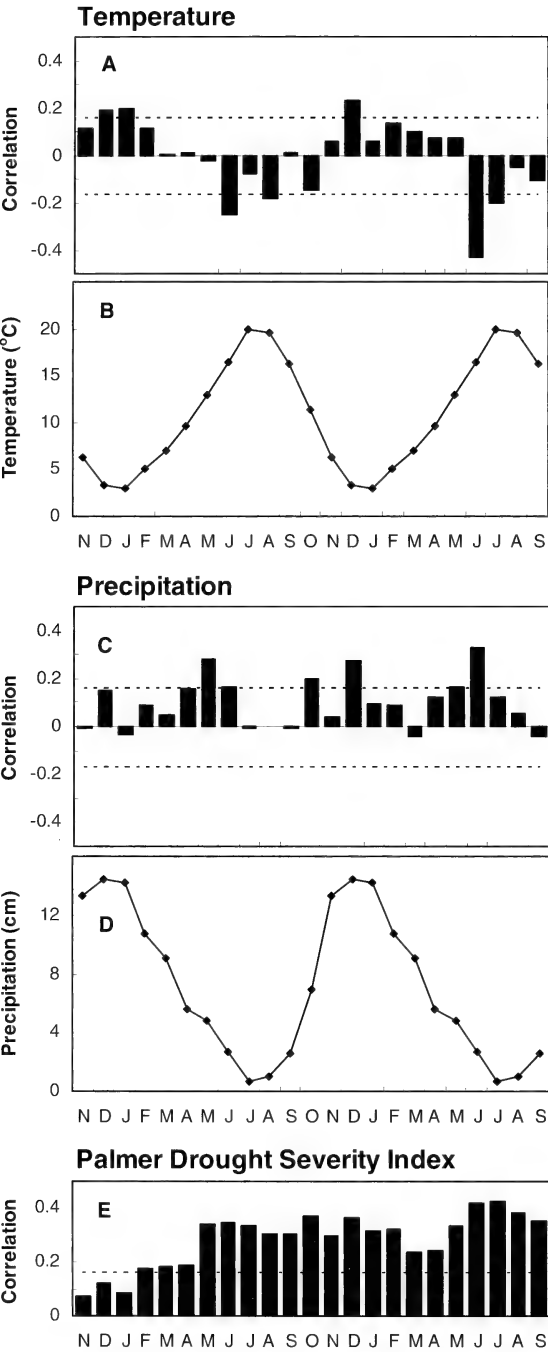


FIG. 4. Pearson correlation coefficients between tree-ring width index and mean monthly A) temperature, (C) precipitation, and (E) PDSI. Graphs B and D show the mean monthly temperature and precipitation, respectively. Climatic data are from the NCDC's Oregon Climate Division 3, spanning from A.D. 1895 to 2000. The horizontal line at 0.165 indicates the critical value ($\alpha = 0.05$).

ring, ranging from 12.5 to 76.9% of the trees sampled. Similarly, the growth index for the 1739 growth ring was below the average of 1.0 for all regional sites, except for Horse Mtn.

DISCUSSION

Climatic Implications

Tree-ring based climatic investigations generally focus on site and species specific conditions where tree-ring growth is known to be limited by a particular climatic factor, allowing for that signal in the growth rings to be maximized (Fritts 1976). Although the Page Mtn. dataset was originally sampled to reconstruct the infection history of *P. lateralis* on Port Orford cedar, the quality of the dataset prompted the creation of the chronology and investigation of the relationship of cedar growth and relevant abiotic factors. The validity of this chronology and crossdatability of Port Orford cedar is supported by the high COFECHA series correlation for the master chronology and the correlation statistics for the standardized chronology, specifically the Expressed Population Signal (EPS). With a quality, responsive chronology in a region that has very few climatic studies and for a species with no known tree-ring chronologies, this study provided important baseline information on both regional climate and species-specific responses.

Our analyses revealed information about which climatic parameters control the radial growth of Port Orford cedar at our main study site in the Siskiyou Mountains (Fig. 4). The consistent, positive correlations for PDSI indicate the importance of soil moisture availability for all months of the year. These results correspond with the geographic distribution of Port Orford cedar being limited to areas that maintain significant soil moisture year-round (Zobel et al. 1985). The annual average of PDSI showed a strong correlation with radial growth, emphasizing the long-term effects of moisture supply for the cedar's growth. Similarly, the analysis for the annual average of precipitation indicates that the cedar has increased growth during wet years. The insignificant relationship for annual temperature reflects the opposite signs of the significant correlations for summer and winter months.

In summer, the Siskiyou Mountains experience hot and dry conditions that are shown here to limit growth of the Port Orford cedar. Specifically, the month of June showed a strong, negative correlation for temperature and a strong, positive correlation for precipitation, indicating the importance of this month for cedar growth. Little et al.'s (1995) analysis of *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir) growth in the Siskiyou Mountains shows similar results for the month of June. Significant negative correlations for July temperature most likely also reveal the limiting effect of summer temperature on moisture, and thus for the radial growth of Port Orford cedar. For PDSI, June and

TABLE 2. SUMMARY RESULTS FOR THE PHYSICAL DAMAGE AND GROWTH INDEX INDICATORS OF AN EXTREME CLIMATIC EVENT IN 1738/1739. Watershed and Geomorphology categories are for data within the Page Mountain study site.

| | Physical damage | | Growth index | | |
|-----------------------------|-----------------|-------------|--------------|-------|-------------|
| | % with damage | Sample size | Growth index | SD | Sample size |
| Page Mountain | 53.5 | 271 | 0.601 | 0.257 | 264 |
| Watershed | | | | | |
| Elder Creek | 56.0 | 141 | 0.617 | 0.244 | 136 |
| Little Elder Creek | 60.0 | 65 | 0.532 | 0.265 | 65 |
| Page Cree | 55.0 | 20 | 0.726 | 0.238 | 20 |
| Dunn Creek | 100.0 | 4 | 0.420 | 0.077 | 4 |
| Poker Creek | 34.1 | 41 | 0.619 | 0.279 | 39 |
| Geomorphology | | | | | |
| Active channel | 47.1 | 17 | 0.568 | 0.258 | 17 |
| Streambank | 59.8 | 82 | 0.609 | 0.252 | 79 |
| Floodplain | 52.8 | 36 | 0.572 | 0.306 | 33 |
| High floodplain | 50.0 | 20 | 0.566 | 0.238 | 19 |
| Terrace | 55.6 | 9 | 0.615 | 0.290 | 9 |
| Hillslope | 63.6 | 22 | 0.519 | 0.203 | 22 |
| Regional | | | | | |
| Page Mountain | 53.5 | 271 | 0.601 | 0.257 | 264 |
| Coquille River Falls | 76.9 | 13 | 0.613 | 0.464 | 12 |
| South Fork Smith River | 50.0 | 4 | 0.732 | 0.265 | 4 |
| Bluff Creek at Fish Lake | 60.0 | 5 | 0.878 | 0.393 | 5 |
| Clear Creek | 46.2 | 13 | 0.710 | 0.277 | 13 |
| South Fork Sacramento River | 12.5 | 16 | 0.847 | 0.388 | 16 |
| Horse Mountain | 0.0 | 3 | 1.109 | 0.298 | 3 |

July are the months with the highest correlations, underscoring the significance of summer soil moisture conditions. A positive correlation for precipitation for both the current and previous May reflect the effect of spring precipitation at the beginning of the growing season when higher temperatures may induce greater transpiration and water use. In summary, our results are in agreement with other studies that have shown the importance of soil moisture for conifer growth in the Pacific Northwest (Robertson et al. 1990), especially during the late spring and summer (Waring and Franklin 1979; Brubaker 1980).

Winters in the Siskiyou Mountains are typified by cool, mediterranean conditions. Our analysis revealed that Port Orford cedar growth is responsive to wet conditions and elevated soil moisture in winter but prefers warmer winter temperatures. Specifically, the month of December showed the strongest correlations. In regards to a growth affinity for warm winter temperatures, our results are similar to Douglas-fir studies in the Siskiyou Mountains (Little et al. 1995) and the Pacific Northwest as a region (Peterson and Heath, 1990). However, unlike Douglas-fir, which can be inhibited by wet conditions in the winter (Little et al. 1995), Port Orford cedar responds positively to wet conditions and soil moisture even in the winter. This may reflect the greater number of pathogens that utilize Douglas-fir (e.g., needle casts), where wet winters may aid in pathogen growth and reproduction (Scharpf 1993). Port Orford cedar has few known pests or

pathogens due to its high volatile oil content and *P. lateralis* is the only pathogen known to cause mortality (Zobel et al. 1985).

Overall, we find radial growth of Port Orford cedar at Page Mountain promoted by high year-round soil moisture, cool and wet conditions in summer (June), and warm and wet conditions in winter (December). With much of southern Oregon and northern California experiencing hot, dry summers, many Port Orford cedars are limited to riparian regions that provide them with required levels of soil moisture (Zobel et al. 1985). Because the cedars sampled for this chronology were originally used to reconstruct the invasion of a water-born disease, this chronology is composed of cedars found in relatively moist, highly infectable areas. While the trees used in our study are representative of the majority of the cedar's population within the study area, creating a chronology from cedars found in more sensitive areas (e.g., drier, upland sites) may allow for a stronger signal to be recognized.

Extent and Potential Cause of the 1738/1739 Climatic Event

The year 1739 was likely affected by anomalous climatic conditions as evidenced by 1739 showing the smallest ring width index for the entire 580-year chronology as a single-year departure from the common pattern (Fig. 3). In over half the cedars with inner-ring dates pre-1739 (Table 2), there was physical damage in the form of abnormal cells and

discoloration to the 1738/1739 ring. Often, deposits of resin extend from after the latewood of 1738 into the earlywood of 1739, pinpointing a trauma event occurring in the dormant season after the 1738 growth season or during the early growing season of 1739. At the Page Mtn. site, the spatial extent of this event was consistent across all five watersheds and across topographic position relative to the stream.

Evidence of the 1738/1739 event in the form of physical damage and below average growth index was found at all of the regional sites sampled except for Horse Mtn. With Horse Mtn. having the fewest trees sampled ($n = 3$) of our regional sites, it is possible that the conditions of the event occurred there but we did not sample a tree that recorded it. It is also possible that the event did not affect this site, perhaps because of its southernmost position among our sampled sites. Frequency of occurrence varied among the sites; however, sampling was not sufficient for evaluating intersite differences in the event's severity. Rather than comparing sites, our intention was to document the occurrence of the event across Port Orford cedar's range. We conclude that the 1738/1739 event did occur on a scale that approximates a large portion of the cedar's range.

In a precipitation reconstruction from drought-sensitive conifers, Graumlich (1987) classified 1739 as a severe, single-year drought for the Pacific Northwest as a whole, with a strong signal for the southern extent that overlaps with the range of Port Orford cedar. That low soil moisture availability (PDSI) and low precipitation have been shown to limit the radial growth of Port Orford cedar and that 1739 is the smallest ring of the entire chronology support the classification of 1739 as a severe, single-year drought for the current study. This extends the range of the 1739 severe, single-year drought event initially classified by Graumlich to include a more western extent. Knapp et al. (2002) examined tree-ring records from *Juniperus occidentalis* spp. *occidentalis* Hook. (western Juniper) to classify extreme, single-year drought events in the interior Pacific Northwest using climatic pointer years from A.D. 1500 to 1998. Although it was not among the top 50 published drought years, the year 1739 ranked 67th (13th percentile) for all sites sampled in this study (Knapp personal communication). This further supports the classification of 1739 as a severe, single-year drought event for the Pacific Northwest, including the southwestern extent captured by the range of Port Orford cedar. A drought reconstruction in central Oregon (Pohl et al. 2002) and tree ring records of precipitation in eastern Oregon (Keen 1937) did not show 1739 as an extreme year, suggesting that the event did not produce a strong signal in areas further inland.

While a below average ring width index for 1739 is ubiquitous for Graumlich (1987), Knapp et al. (2002), and our current study, this year is unique

for Port Orford cedar in regards to the physical damage found in cedars across its range. Here, we examine the potential cause of this trauma event. Considering that the event affected Port Orford cedars throughout the range of the species, a fire of such scale would be recognizable in other tree-records of the area. The lack of such evidence discounts fire as a possible cause (Taylor and Skinner 2003; Skinner personal communication 2003). Dendrochronological records show an outbreak of heart rot in western juniper in the Pacific Northwest occurring between 1730 and 1749; however, damage to the cedars indicate a strong single-year event, not a multi-year event (Knapp and Soulé 1999). Furthermore, there are no known diseases or pests that can significantly suppress radial growth in Port Orford cedar. The invasion by the fatal pathogen *P. lateralis* was not occurring prior to 1952 (Hansen et al. 2000).

Another potential cause for the damage is a regional freezing event. During a freeze, tissues contract and can cause the crushing of cambial cells and the formation of a frost ring (Glerum and Farrar 1966). LaMarche and Hirschboeck (1984) linked the formation of frost rings with the cooling effect created from stratospheric aerosol veils produced from volcanic eruptions. Although a major volcanic eruption occurred in 1739 on Mt. Tarumai (Shikotsu) on the Japanese island of Hokkaido, this eruption has been dated after the spring of 1739, excluding it as a cause of the damage to the cedars (Simkin and Siebert 1994). The possibility of a regionally extending frost event, independent of volcanic activity, is still a consideration for the cause of the damage to the cedars.

That the strongest physical damage of the cedar chronology coincides with the smallest ring width index (severe, single-year drought) presents the possibility that the trauma event was linked to drought conditions. Although the drought is evident in the growth ring for 1739, the conditions likely existed in the dormant season prior to growth. Injury could occur in the winter or early spring if, for example, replenishment of water deficiencies is prevented by a prolonged frost (Larcher 1980). Such an event is sensible considering that much damage to Port Orford cedars occurs in dry, windy, cold weather, where desiccation is a key parameter (Zobel et al., 1985). Although the cause of the 1739 physical damage is inconclusive, we believe that the most likely cause is a frost event coupled with a dry year.

SUMMARY

We have created a quality, responsive chronology for Port Orford cedar in the Siskiyou Mountains of southwestern Oregon and northern California that spans from A.D. 1420 to 2000. This dataset represents the first standardized tree-ring chronology established for Port Orford cedar and shows

this species to be suitable for dendroclimatological studies. The radial growth of Port Orford cedar was correlated with soil moisture availability year-round that corresponds with the cedar's distribution. Hot and dry summer conditions in the Siskiyou Mountains were both found to limit the cedar's growth. Port Orford cedar growth showed an affinity for warm winter temperatures, as other studies have found to be true for Douglas-fir in the Siskiyou Mountains. However, unlike Douglas-fir, the cedar was responsive to wet winter conditions, emphasizing the cedar's strong dependence on soil moisture year-round. The year 1739 consistently showed a small ring width and physical damage to the earlywood for cedars across the spatial extents of the Page Mtn. site and also across most of the range of the cedar. The conspicuously small size of the 1739 growth ring has been linked to a single-year, severe drought that affected the Pacific Northwest. This study extends the range of this drought to include the southwestern portion of the Pacific Northwest that is represented by Port Orford cedar. The trauma event represented by the physical damage was pinpointed to have occurred in the dormant winter season of 1738 or during the early spring of 1739 and is possibly indicative of a frost event associated with the weather conditions of a drought year.

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SEED GERMINATION OF *ERODIUM MACROPHYLLUM* (GERANIACEAE)

IAN G. GILLESPIE^{1,2} AND HALLY M. ANDERSEN¹

Department of Botany and Plant Sciences, University of California,
Riverside, CA 92521

Key Words: seed germination, scarification, *Erodium macrophyllum*, filaree, seed dormancy.

Mechanisms that break dormancy in seeds are of interest on both an ecological level and for applied purposes when trying to maximize germination of seeds used in restoration efforts. Ecologically, understanding seed dormancy can provide insight into life-history strategies and evolutionary patterns (Templeton and Levin 1979; Baskin and Baskin 1998). For restoration studies, understanding seed biology can ultimately result in improved restoration (McDonald 1993). Unfortunately, for many species, especially those that are rare, we often lack the data necessary to understand what treatments, if any, will affect seed dormancy. We experimentally tested how 10 treatments would affect the germination of seeds from the rare native California grassland forb, *Erodium macrophyllum* Hook. & Arn. (large-leaved filaree, Geraniaceae).

Erodium macrophyllum is a rare annual forb found in small populations throughout the California floristic province (Gillespie 2005). Although it was likely once more common, it has become exceedingly rare in many parts of California. It is found in exotic and native grasslands and coastal sage scrub. Like many of California's native forbs, seeds of *E. macrophyllum* germinate in the fall or early winter at the onset of rain and the plants grow, reproduce and then senesce in spring. We studied *E. macrophyllum* because previous work indicated that restoration of this species can be inhibited by poor germination (Gillespie and Allen 2004). Given that very little is known about *E. macrophyllum* seed dormancy we used 10 different treatments in hopes of finding at least one that may increase germination.

Treatments consisted of stratification, heat, three different concentrations of smoke water, gibberellic acid, sulfuric acid, scarification, removal of the pericarp and a control that received no treatment. These treatments were chosen because they are sometimes known to affect seed dormancy (Baskin and Baskin 1998; Montalvo et al. 2002). The pericarp removal treatment was specifically chosen because they can fall off after extensive handling of the seeds (Gillespie personal observation). The

seeds came from approximately 20 plants grown in a greenhouse and the original seed source came from a population of *E. macrophyllum* in western Riverside County, California (33.7416°N, 117.4387°W; elevation 365 m). The experiment was carried out in a laboratory where the temperature was kept between approximately 20–23°C. For each treatment, 10 seeds were placed in a plastic Petri dish (9 cm diameter) between two pieces of filter paper. Each treatment was replicated 10 times in Petri dishes (10 treatments × 10 replicates = 100 Petri dishes). The filter paper was kept moist with distilled water added as needed throughout the duration of the study. Seeds were monitored every 2–3 days from 18 November 2002 to 15 December 2002. When a seed was found to be germinating (i.e., at least the emerging radicle was visible) it was removed from the dish. A one-way analysis of variance (ANOVA) was used to determine if the germination amounts differed between treatments. The details of each treatment are as follows:

Stratification. Seeds were placed in dry Petri dishes in a refrigerator at 9°C from 15 October to 15 November 2002.

Heat. Seeds were placed in glass Petri dishes in a drying oven at 40°C from 15 October to 15 November 2002. Later seeds were transferred into plastic Petri dishes.

Smoke water. Three different dilutions of smoke water were used: 1:10, 1:100 and 1:1000 (E. Allen personal communication). The dilutions were made with distilled water and Liquid Smoke (Colgin, TX, USA). For each of the three different treatments the seeds were soaked in their appropriate diluted smoke water for 24 hrs one day before the study started.

Gibberellic acid. 5 ml of Gibberellic acid (50 ppm) was added to each of the 10 Petri dishes when the experiment was started.

Sulfuric acid. The seeds were soaked in concentrated sulfuric acid for 60 seconds and then rinsed in distilled water before being added to Petri dishes.

Scarification. The pericarp was removed from each seed and then the seed coat was nicked with a razor blade.

¹ Present address: 181 Westminster Road, Putney, VT 05346.

² Author for correspondence, email: ian@iggsoftware.com

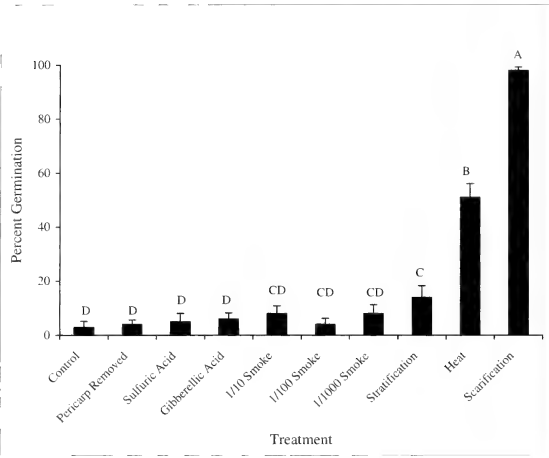


FIG. 1. Percent germination of seeds from the rare forb *Erodium macrophyllum* under ten different treatments. Different letters between bars indicate a significant difference ($P < 0.05$). Data are means \pm one standard error, $n = 10$.

Pericarp removal. The pericarp was removed from each seed to control for the scarification treatment.

Control. These seeds were not manipulated except for being put in 10 Petri dishes in moist filter paper.

The scarification treatment had the greatest effect on seed germination (Fig. 1). Heat, although not as effective as the scarification treatment, increased germination by 48% compared to the control. The stratification treatment also increased germination compared to the control, sulfuric acid, pericarp removal and the 1:100 smoke water treatments. No other treatments significantly increased germination (Fig. 1).

Our results have implications for *E. macrophyllum* seeds in wild populations. For example, the heat treatment, although lasting for only 30 days,

is similar to what a seed might experience during the hot, dry summers of California and our results suggest that such an exposure may affect subsequent germination of *E. macrophyllum* seeds. Given this, it is possible that the severity of summer heat may influence subsequent *E. macrophyllum* recruitment the following wet season. The results from the scarification treatment suggest that germination of *E. macrophyllum* may be enhanced by physical abrasion to the seed coat. Abrasion to the seed may occur when the seeds drill themselves into the ground using their awns which coil and uncoil in response to changing moisture levels (Gillespie personal observation). However, it is likely that this abrasion does not greatly increase germination, at least in some soil types (Gillespie and Allen 2004). If land managers and restorationists use seed to introduce *E. macrophyllum* at a restoration or mitigation site, heating or scarifying the seeds provides for an inexpensive and effective way to maximize germination.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

CAREX PENDULA Hudson (CYPERACEAE).—BUTTE CO., mostly at the edge of the water, shaded by large valley oaks on bank and alders, forming discrete dense clumps, south side of city of Chico, along Comanche Creek (Edgar Slough) just SW of Meyers Ave, 195 ft, T22N R1E S36 SW¼, 23 Oct. 1989, *L. P. Janeway 3652* (CAS, CHSC, WS; the CAS dup det. A. A. Reznicek 26 Feb. 2003); shaded by riparian forest of valley oak, sycamore, forming massed dense clumps along edge of S side of creek, along Comanche Creek (Edgar Slough) behind the office of USFS Tree Improvement Center, 225 ft, T21N R2E S5 NW¼, 12 Jan. 1989, *L. P. Janeway 3653* (CHSC, WS); growing at the edge of the creek, often with blackberry brambles and partial shade from alders and valley oaks, common small patches and clumps of this along the creek edge, south end of Chico, along edge of Comanche Creek at the bicycle bridge (former railroad bridge) about 150 m southeast (upstream) of the Midway (road) bridge across the creek, 59 m, T22N R1E S36 SW¼ of SE¼, 39°42'47"N, 121°48'43"W, 20 June 2004, *L. P. Janeway 8137* (CDA, CHSC, JEPS, MICH).

Previous knowledge. Introduced from Europe; in North America previously only reported as naturalized at low elevation (less than 20 m) in Virginia and Washington (A. A. Reznicek, 2002, in *Flora of North America North of Mexico*, Volume 23, Magnoliophyta: Commelinidae (in part): Cyperaceae). This striking large clump-forming species is sold in the horticultural trade for water gardens, especially in the U.S. southeast. The first two collections noted above were originally identified as *Carex spissa* (L. P. Janeway, 1992, *Cyperaceae of Butte County, California*, Part 1: *Carex*). Janeway (loc. cit.) suggested that the original introduction was at the USFS Tree Improvement Center (now the Genetic Resource and Conservation Center) along Comanche Creek, the most upstream site at which the species was found. At that time the species was well established, in decreasing amounts, along 5 miles of Comanche Creek downstream of the Center. The third collection shows that the species is still well-established along Comanche Creek. This should be watched for its invasive potential downstream and into the Sacramento River.

Significance. First reports for California.

—LAWRENCE P. JANEWAY, Biological Sciences Herbarium, California State University, Chico, Chico, CA 95929-0515.

CALIFORNIA

DELPHINIUM SCAPOSUM Greene (RANUNCULACEAE).—San Bernardino Co., east side of Whipple Mountains: Just north of Gene Pumping Station along Black Meadow Landing Road, in a steep, rocky canyon through light-colored granite. Boulder-strewn slope above wash, ± north-facing. Some associated species were *Larrea tridentata*, *Fouquieria splendens* ssp. *splendens*, *Opuntia basilaris*, *O. acanthocarpa* var. *coloradensis*, *Hyptis emoryi*, *Encelia farinosa*, *Asclepias albicans*, *Trix-*

is californica var. *californica*, and *Peucephyllum schottii*. 34°18.219'N, 114°11.337'W, 269 m (881 ft). Gene Wash 7.5' quadrangle. 17 March 2003, *S. J. De Groot & J. M. Porter 1411* (RSA; duplicate to be distributed); 29 March 2004, *S. J. De Groot 3964* (RSA); 11 April 2004, *S. J. De Groot 4128* (RSA; duplicate to be distributed).

Whipple Mountains: Ridge near highest peak, west side of the main part of the range, rocky slopes and outcrops. Associated with *Larrea tridentata*, *Krameria erecta*, *Lycium fremontii*, *Aloysia wrightii*, *Eriogonum fasciculatum* var. *polifolium*, *Galium stellatum* var. *eremicum*, and *Cheilanthes parryi*. 34°18'42"N, 114°24'10"W. 1055 m (3463 ft). Whipple Mountains SW 7.5' quadrangle. 15 March 2004, *S. J. De Groot, K. De Groot, L. Lubinsky, L. L. Worlow 3627* (RSA).

Whipple Mountains: Wash south of highest peak, west side of the main part of the range, rocky bank of wash. Associated with *Mirabilis bigelovii* var. *retrorsa*, *Lycium andersonii*, *Muhlenbergia porteri*, *Eriogonum inflatum*, *Ditaxis neomexicana*, *Pholistoma auritum* var. *arizonicum*, *Larrea tridentata*, and *Krameria erecta*. 34°18'18"N, 114°23'59"W. 834 m (2737 ft). Whipple Mountains SW 7.5' quadrangle. 14 March 2004, *S. J. De Groot, K. De Groot, L. Lubinsky, L. L. Worlow 3590* (RSA).

Previous knowledge. *Delphinium scaposum* has been recorded from Arizona, New Mexico, Utah, Nevada, Colorado, and Sonora, Mexico (Welsh et al. 1987, Great Basin Naturalist Mem. 9:508–509; Kearney and Peebles 1960, Arizona Flora, University of California Press, Berkeley; Shreve and Wiggins 1964, Flora and Vegetation of the Sonoran Desert, Stanford University Press, Stanford). The species was originally described from New Mexico (Greene 1881, Bot. Gaz. 6:156–157). Typical habitats include grasslands, juniper woodlands, open deserts, gravelly mesas, and rocky or brushy ravines between 1200 and 2700 m (Warnock 1997, *Delphinium*, Fl. N. Amer. 3: 215, Oxford University Press, New York; Kearney and Peebles 1960; Ewan 1945, Univ. Colo. Phys. & Biol. Studies 2(2):55–244). It is generally found in sandy or gravelly soil (Kearney and Peebles 1960).

The nearest recorded collection sites are in Arizona along the Bill Williams River (*Munz 16640*, POM 303068) and the Colorado River, with no indication that *D. scaposum* may occur in California (Kearney and Peebles 1960; Ewan 1945). Another Arizona collection (*M. E. Jones s.n.*, 21 April 1903, POM 100717), cites the location “Chimehuevis,” but this was an earlier name for the range now known as the Mohave Mountains, which lie to the northeast of Lake Havasu City in Arizona (Granger 1983, *Arizona's Names*, Falconer Publications, Tucson; Barnes 1935, *Arizona Place Names*, University of Arizona Bulletin 6(1), University of Arizona, Tucson; Jones 1908, Contr. W. Bot. 12:16, 50, 66; Lee W. Lenz personal communication).

Ewan (1945) distinguishes two races, a strictly scapose form with royal blue flowers that occurs along the Gila River drainage and Mogollon Mesa (race a), and a subscapose, often branching form with lighter blue flowers that occurs on the Colorado Plateau and Colorado River drainage (race b). The plants recently collected in the Whipple Mountains had royal blue flowers and a strictly scapose habit (race a), but were collected in the Colorado

River drainage (race b). The original material may have dispersed from the Gila drainage, but given the widely scattered occurrences of *D. scaposum* in the Whipple Mountains, this most likely did not happen in very recent history.

Significance. This is the first reported occurrence of *D. scaposum* from California. All of the collections were made from elevations below 1200 m, the species' presumed lower limit.

ERIGERON OXYPHYLLUS Greene (ASTERACEAE).—San Bernardino Co., east side of Whipple Mountains Wilderness area: chute below summit of Cupcake Butte, north of Whipple Wash. Plants were scattered among boulders in steep, narrow chute, approximately north facing. Also in the area were *Teucrium glandulosum*, *Cymopterus panamintensis* var. *acutifolius*, *Pleuraphis rigida*, *Pleurocoronis pluriseta*, *Machaeranthera pinnatifida* ssp. *gooddingii*, and *Matelea parviflora*. 34°20'49"N, 114°19'28"W, 790 m/2590 ft. Whipple Wash 7.5' quadrangle, T3N R2E center of sec. 14. 10 October 2003, Sarah J. De Groot & J. Mark Porter 3315 (RSA, duplicates to be distributed).

Whipple Mountains: North facing slope just north of summit, steep slope of loose rock and boulders. With *Antirrhinum filipes* and *Prenanthes exigua*. 34°19'55"N, 114°25'13"W, 646 m/2120 ft. Whipple Mountains SW 7.5' quadrangle, T3N, R24E, S half of line between sect. 23 and 24. 9 May 2004, Sarah J. De Groot 4286a (RSA, duplicates to be distributed).

Previous knowledge. *Erigeron oxyphyllus* has been found in Maricopa, Mohave, Pinal, and Yuma counties, Arizona, and in Sonora, Mexico (Nesom 1992, *Phytologia* 72(3):194–195; Shreve and Wiggins 1964; Kearney and Peebles 1960). The type collection is from Yucca, in Mohave county (Nesom 1992; Greene 1895, *Erythea* 3(2): 20). Typical habitat is dry rocky hillsides, occasionally by seeps or streams, between 610 and 915 m (2000–3000 feet; Nesom 1992; Shreve and Wiggins 1964; Kearney and Peebles 1960).

Significance. This is the first report of *E. oxyphyllus* in California. Habitat was characteristic of sites where it is found in Arizona.

Thanks to J. Mark Porter for double-checking determinations.

—SARAH J. DE GROOT, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711.

CALIFORNIA

HOITA MACROSTACHYA (DC.) Rydb. (FABACEAE).—Shasta Co., Little Backbone Creek inlet, Lake Shasta, approximately 4.4 km northwest of Shasta Dam in ponderosa pine/deerbrush habitat. Associated species include *Pinus ponderosa*, *Ceanothus integerrimus*, *Arctostaphylos viscida*, *Toxicodendron diversilobum*, and *Rubus discolor*. Bohemotash Mountain USGS 7.5' quadrangle, T34N R5W SE¼ of SE¼ sect. 33, UTM 10 0548086E 4511789N, elevation 329 m, 31 July 2003, L. Lindstrand III, K. Youngblood, s.n. (North State Resources Herbarium [North State Resources, Inc. Herbarium, 5000 Bechelli Lane, Suite 203 Redding, CA 96002; private]; JEPS).

Mainstem of Lake Shasta between Little Backbone

Creek and Butcher Creek, approximately 3.2 km northwest of Shasta Dam in mixed willow habitat. Associated species include *Salix exigua*, *Salix lucida*, *Rubus discolor*, *Pinus ponderosa*, *Arctostaphylos viscida*, and *Toxicodendron diversilobum*. Shasta Dam USGS 7.5' quadrangle, T33N R5W NW¼ sect. 3, UTM 10 0548833E 4510649N, elevation 329 m, 31 July 2003, L. Lindstrand III, K. Youngblood, s.n. (North State Resources Herbarium [private]; JEPS).

City of Redding, Oregon Gulch, at the Oregon Gulch/Eastside Road crossing, approximately 0.75 km miles north of the Bonnyview Road/Highway 273 intersection in mixed riparian habitat. Associated species include *Salix exigua*, *Salix lucida*, *Salix gooddingii*, *Rubus discolor*, *Polygonum* sp., *Cyperus* sp., and *Vitis californica*. Redding USGS 7.5' quadrangle, T31N R5W San Buenaventura Land Grant Boundary, UTM 10 0552005E 4488352N, elevation 183 m, 8 October 2004, L. Lindstrand III, s.n. (North State Resources Herbarium [private]; Shasta-Trinity National Forest Herbarium [Shasta-Trinity National Forest Herbarium, 3644 Avtech Parkway, Redding, CA 96002]; JEPS).

Previous knowledge. *Hoita macrostachya* was apparently collected only once from Shasta County, more than a century ago (M. S. Baker #286, July 5, 1898; JEPS 65632). This represents the northernmost-recorded extent of the species, whose range is restricted to California and Baja California (J. C. Hickman, 1993, *The Jepson manual: higher plants of California*, University of California Press, Berkeley, CA). The species was seen in vegetative condition by the second author in the Charlie Creek watershed, tributary to the upper Sacramento Arm of Lake Shasta, Lamoine USGS 7.5' quadrangle, T35N R5W NE¼ S22, elevation 366 m, on 5 May 2000. Without flowers or fruit, this mystery plant was tentatively identified as *Hoita macrostachya*, but no voucher was made. Subsequently, the species was observed by the primary author near Salt Creek in a roadside wetland/ditch along Statton Road, northeast of the Salt Creek Group Campground, O'Brien USGS 7.5' quadrangle, T35N R4W SW¼ S28, elevation approx. 365 m, during October 2003 but no voucher was made. During field investigations in 2003, North State Resources personnel collected a piece of *Hoita macrostachya* fruiting material for identification from the west side of Lake Shasta. The second author reviewed the material in the North State Resources office, which confirmed her earlier identification of the Charlie Creek material, and rekindled curiosity about the distribution of *Hoita macrostachya* in Shasta County. It was therefore of interest when North State Resources personnel found more *Hoita macrostachya* during further field investigations in 2003 and 2004 around the perimeter of the west side of Shasta Lake, near Salt Creek, and in the city of Redding.

Significance. *Hoita macrostachya* is still extant in Shasta County, though uncommon. The species has been collected or seen from five locations, all in the foothill drainages of the upper and lower Sacramento River along permanent or seasonal streams, or spring/seep features. Elevations at these locations range from 183 meters at Oregon Gulch to 366 meters at Charlie Creek.

NEVIUSIA CLIFTONII J. R. Shevock, B. Erter, & D. Taylor.

¹ North State Resources, Inc. Herbarium, 5000 Bechelli Lane, Suite 203 Redding, CA 96002.

² Shasta-Trinity National Forest Herbarium, 3644 Avtech Parkway, Redding, CA 96002.

(ROSACEAE).—Shasta Co., Rippgut Creek, approximately 0.51 km north of confluence with Pit River arm, Lake Shasta, in montane hardwood-conifer habitat (no limestone present). Associated species include *Pseudotsuga menziesii*, *Quercus chrysolepis*, *Acer macrophyllum*, *Cornus nuttallii*, *Corylus cornuta*, *Cercis occidentalis*, *Rosa* sp., *Styrax officinalis*, *Rhus trilobata*, *Aristolochia californica*, *Symphoricarpos albus*, *Rubus ursinus*, *Toxicodendron diversilobum*, *Osmorhiza chilensis*, *Trillium chloropetalum*, *Adiantum jordanii*, and *Asarum hartwegii*. Devil's Rock USGS 7.5' quadrangle, T34N R2W SW¼ of SE¼ sect. 2, NAD 27, UTM 10 0579245E 4519478N, elevation 350 m, 23 June 2003, L. Lindstrand III, s.n. (Shasta-Trinity National Forest Herbarium [Shasta-Trinity National Forest Herbarium, 3644 Avtech Parkway, Redding, CA 96002]).

Stein Creek, at the confluence with Pit River arm, Lake Shasta, in montane hardwood-conifer habitat (no limestone evident). Associated species include *Pseudotsuga menziesii*, *Quercus chrysolepis*, *Acer macrophyllum*, *Cornus nuttallii*, *Corylus cornuta*, *Taxus brevifolia*, *Philadelphus lewisii*, *Toxicodendron diversilobum*, *Aesculus californica*, *Adiantum jordanii*, and *Asarum hartwegii*. Devil's Rock USGS 7.5' quadrangle, T34N R2W SW¼ sect. 14, NAD 27, UTM 10 0578663E 4516697N, elevation 329 m, 1 Sept. 2004, J. K. Nelson 2004100, with L. Lindstrand III (Shasta-Trinity National Forest Herbarium; JEPS).

Brock Creek, at the confluence of an unnamed tributary to Brock Creek and the Brock Creek inlet, Pit River arm, Lake Shasta, associated with a limestone outcrop in montane hardwood-conifer habitat. Associated species include *Pseudotsuga menziesii*, *Pinus ponderosa*, *Quercus garryana*, *Acer macrophyllum*, *Philadelphus lewisii*, *Toxicodendron diversilobum*, *Aesculus californica*, and *Adiantum jordanii*. Devil's Rock USGS 7.5' quadrangle, T34N R2W SW¼ of SW¼ sect. 1, NAD 27, UTM 10 0576890E 4518004N, elevation 329 m, 1 Sept. 2004, J. K. Nelson 2004101, with L. Lindstrand III (Shasta-Trinity National Forest Herbarium; JEPS).

Unnamed stream south of Cove Creek at confluence with Lake Shasta, Pit River Arm, approximately 1.8 km north of Bear Mountain, in ponderosa pine and blue oak-foothill pine habitat (no limestone evident). Associated species include *Pinus ponderosa*, *Quercus wislizeni*, *Fraxinus latifolia*, *Fraxinus dipetala*, *Quercus garryana* var. *breweri*, *Rhamnus* sp., *Cercis occidentalis*, *Philadelphus lewisii*, and *Toxicodendron diversilobum*. Project City USGS 7.5' quadrangle, T33N R4W SE¼ sect. 1, NAD 27, UTM 10 0561797E 4510091N, elevation 332 m, 1 September 2004, J. K. Nelson 2004102, with L. Lindstrand III (Shasta-Trinity National Forest Herbarium; JEPS).

Blue Ridge, Pit River Arm, Lake Shasta, approximately 1.3 km east of Allie Cove, in montane hardwood-conifer habitat (no limestone evident). Associated species include *Pinus ponderosa*, *Pinus sabiniana*, *Quercus wislizeni*, *Quercus kelloggii*, *Cercis occidentalis*, *Philadelphus lewisii*, *Cornus sessilis*, *Calycanthus occidentalis*, *Vitis californica*, and *Toxicodendron diversilobum*. O'Brien USGS 7.5' quadrangle, T34N R4W NW¼ sect. 36, NAD 27, UTM 10 0561059E 4511874N, elevation 329 m, 1 September 2004, J. K. Nelson 2004103, with L. Lindstrand III (Shasta-Trinity National Forest Herbarium; JEPS).

Blue Ridge, Pit River Arm, Lake Shasta, approximately 1.1 km east of Allie Cove, in ponderosa pine habitat (no limestone evident). Associated species include *Pinus ponderosa*, *Quercus kelloggii*, *Quercus chrysolepis*, *Acer macrophyllum*, *Cercocarpus betuloides*, *Quercus garryana* var. *breweri*, *Vitis californica*, *Cercis occidentalis*, *Quer-*

cus wislizeni, *Philadelphus lewisii*, *Calycanthus occidentalis*, and *Toxicodendron diversilobum*. O'Brien USGS 7.5' quadrangle, T34N R4W NE¼ sect. 35, NAD 27, UTM 10 0560912E 4512087N, elevation 329 m, 1 September 2004, J. K. Nelson 2004105, with L. Lindstrand III (Shasta-Trinity National Forest Herbarium; JEPS).

Keluche Creek, at the confluence with Lake Shasta, McCloud River Arm, approximately 3 km south of Hirz Bay, in ponderosa pine habitat (no limestone evident). Associated species include *Pinus ponderosa*, *Quercus garryana* var. *breweri*, *Pseudotsuga menziesii*, *Umbellularia californica*, *Styrax californica*, *Vitis californica*, *Acer macrophyllum*, *Calycanthus occidentalis*, *Rubus ursinus*, *Quercus kelloggii*, *Quercus chrysolepis*, *Corylus cornuta*, and *Toxicodendron diversilobum*. O'Brien USGS 7.5' quadrangle, T35N R4W SE¼ sect. 35, NAD 27, UTM 10 0560875E 4521116N, elevation 329 m, 1 September 2004, J. K. Nelson 2004106, with L. Lindstrand III (Shasta-Trinity National Forest Herbarium; JEPS).

Previous knowledge. The original descriptions and information of *N. cliftonii* (Novon 2(4):284–289, 1993; *Fremontia* 22(3):3–13, 1993) and the current California Flora (J. C. Hickman, 1993, The Jepson manual: Higher plants of California, University of California Press, Berkeley, CA) note the species occurring in habitats associated with limestone rock formations. The California Department of Fish and Game's California Natural Diversity Database and the California Native Plant Society's Inventory (Rare Plant Scientific Advisory Committee, [October 3, 2004 data date version], Inventory of rare and endangered plants, California Native Plant Society, Sacramento, CA) contain records of ten known locations (excluding the locations discussed herein). Of these ten previously known locations, eight (80%) occur within habitats associated with limestone rock formations.

Significance. These seven new collections nearly double the number of known *N. cliftonii* locations. Additionally, these new discoveries show that nearly one-half (47%) of the known species locations occur in habitats not associated with limestone rock formations.

We thank the U.S. Bureau of Reclamation Mid-Pacific Region office for their support.

—LEN LINDSTRAND III, Fisheries/Wildlife Biologist, Project Manager, North State Resources, Inc., 5000 Bechelli Lane, Suite 203, Redding, CA 96002. lindstrand@nsrnet.com; JULIE KIERSTEAD NELSON, Forest Botanist, Shasta-Trinity National Forest, 3644 Avtech Parkway, Redding, CA 96002. jknelson@fs.fed.us

IDAHO

CRUPINA VULGARIS Cass. (ASTERACEAE).—Idaho Co., Circle C Ranch, Hells Canyon National Recreation Area (NRA), ca. 2 km northeast of Pittsburg Landing on the Snake River, canyon grassland of *Sporobolus cryptandrus*/*Aristida longiseta* (10% cover), associated species: *Bromus commutatus*, *Sisymbrium altissimum*, *Plantago patagonica*, *Lactuca serriola*, *Chondrilla juncea*, *Erigeron pumilus*; UTM 11T 541346E 5054157N NAD27, 463 m, 18 June 2004, Gene Yates USFS #1005 (OSC).

Previous knowledge. Although *Crupina vulgaris*, native to the Mediterranean region, was first discovered in Idaho in 1968 (Stickney 1972, Madroño 21:402), populations in Hells Canyon were not reported until 2003 (Madroño 51: 333). This small population (ca. 500–1000 m²) was dis-

covered on 19 May 2004 by Dan Sharratt, Oregon Department of Agriculture, while assisting a Forest Service weed management group in the release of biological control agents for *Linaria dalmatica* at a *Mirabilis macfarlanei* site across the Snake River (G. Yates personal communication). The closest previously known site on the Snake River was at Garden Creek, about 65 km north of Pittsburg Landing. A population at Pine Bar on the Salmon River lies about 30 km north of Pittsburg Landing, but is much farther as measured either by road or river routes. Not collected, but another population of *Crupina vulgaris*, about 0.2 ha in size, was discovered by Dan Sharratt on 13 May 2003 on the Idaho side of the river between RM200 and RM201 near the mouth of Camp Creek, about 0.4 km downriver from the mouth of Dry Creek (45.7853°N, 116.6288°W). This privately owned site lies about 24 km downriver from Pittsburg Landing.

Significance. The area around Pittsburg Landing has been grazed by cattle and sheep since the 1880s, when small homesteads were established. From 1891 through 1933 the Pittsburg ferry provided transportation across the Snake River to the wagon road from White Bird, Idaho, that was completed in 1900 (Carrey et al. 1979, Snake River of Hells Canyon, Backeddy Books, Cambridge, ID). Wood sold his holdings to the Nez Perce Sheep Company, one of the largest sheep operations in the Canyon, owned up to 200,000 head of ewes in the 1920s (Carrey et al. 1979), of which several thousand were grazed in the Pittsburg area (Baumgarten, Hells Canyon NRA, personal communication). The Circle C Cattle Company purchased the land from the Nez Perce Sheep Company in the early 1930's, and used the land for winter grazing for their cattle operation (E. Baumgarten personal communication). Circle C Ranch was purchased as part of the creation of Hells Canyon NRA in 1973 and Jayo Ranches secured the Forest Service grazing permit, continuing to use it for winter forage until the permit was cancelled in 2002 (E. Baumgarten personal communication).

In the Salmon River drainage just to the east of Hells Canyon NRA, four populations of *Crupina vulgaris* were discovered from 1997 to 2000 between Grangeville and Riggins (L. Lake, Nez Perce NF, personal communication). These included a population 2 km east of Whitebird on Banner Ridge (45°44.506'N, 116°16.785'W), occupying a waste area near a hayfield at 750 m in 1999; 12 ha around a hayfield south of Rhett Creek at 1050 m (45°37.7'N, 116°19.4'W) in May 1997; 16 ha on south-facing grassland along Sherwin Creek at 1050 m (45°35.9'N, 116°19.3'W) in May 2000; and 2 ha of south-west-facing grassland along the Salmon River at 670 m (45°35.3'N, 116°18.8'W), also in May 2000. The latter three sites lying west of the Salmon River between Slate Creek and Lucile, managed by Jayo Ranch (C. Crabtree, Idaho County Weed Program, personal communication), are a probable source for the introduction at Pittsburg Landing.

—CINDY T. ROCHÉ, 109 Meadow View Drive, Phoenix, OR 97535.

OREGON

AEGILOPS CYLINDRICA Host. (POACEAE).—Jackson Co., Sky King Cole Ranch, dominant grass on lower side of road Pilot Rock Road for about a km. T40S R2E sect. 33 W.M., 42°02.917'N, 122°35.238'W, 1440 m, 26 June 2004, *Cindy Talbott Roché s.n.* (OSC).

Previous knowledge. A widespread weed of cereal crops, this species is established in the wheat-growing region of northeastern Oregon, including Baker, Umatilla, Union, and Wallowa counties.

Significance. Jointed goatgrass, a class B Noxious Weed in Oregon, had not been previously reported in Jackson County. This is the first report west of the Cascade Mountains in Oregon. A probable source of introduction is straw mulch used in a revegetation project.

AEGILOPS TRIUNCIALIS L. (POACEAE).—Josephine Co., between Cave Junction and O'Brien on Highway 199 on the east side of the road at the bridge at Rough and Ready Creek, and also along the pullout road for about 0.2 km, associated species: *Ceanothus cuneatus*, *Bromus hordeaceus*, *Aira caryophyllea*; T40S R8W NE sect. 18 W.M., 42°05.562'N, 123°41.015'W, 420 m, 17 June 2004, *Armand Rebeschke and Robert Hartwein s.n.* (OSC).

Previous knowledge. Discovered by Nick Ott in a vegetation survey contracted by Oregon Department of Transportation, the barbed goatgrass site was reported to Ken French, Oregon Department of Agriculture SW Oregon IVM Specialist, on June 7, 2003. This species is native to the eastern Mediterranean and was previously known only from California and western Nevada (in the USA).

Significance. Barbed goatgrass is listed as a Class A Noxious Weed in Oregon. This is the first report in the state documented by a collection. It may have been introduced via vehicular traffic from California.

—CINDY T. ROCHÉ, 109 Meadow View Drive, Phoenix, OR 97535 and ARMAND REBISCHKE, 3040 Biddle Road, Medford, OR 97504.

WASHINGTON

CRYPTANTHA GRACILIS Osterh. (BORAGINACEAE).—Grant Co., Grand Coulee, Sun Lakes State Park, near Dry Falls Lake, near base of rimrock, in soil pocket in talus slope. With *Eriogonum niveum*, *Thelypodium laciniatum*, *Bromus tectorum*, *Epilobium minutum*, 165° azimuth, 50% slope, 410 m elevation, T24N R28E S6, 25 April 1998, *Kathryn A. Beck & Florence E. Caplow 98005* (WTU); Grant Co., Beezley Hills, dry rocky creek bottom, with *Balsamorhiza careyana*, *Lupinus sulphureus*, *Lomatium dissectum*, *Artemisia tridentata*, *Bromus tectorum*, 260° azimuth, 30% slope, 775 m elevation, T21N R28E S13, 29 April 1998, *Kathryn A. Beck & Florence E. Caplow 98007* (WTU); Grant Co., low rounded hills north of Beezley Hills in steep, dry eroding, largely unvegetated sidedraw of main hills, with *Eriogonum strictum*, *Eriogonum compositum*, *Achillea millefolium*, *Poa secunda*, *Phoenicallis cheiranthoides*. Several hundred small plants growing in orange brown soil, 160° azimuth, 70% slope, 845 m elevation, T22N R24E S28, 10 May 1999, *Kathryn A. Beck 99001* (WTU).

Previous knowledge. This taxon is known from Oregon, Idaho, California and most other western states.

Significance. These represent the first known collections of *C. gracilis* in Washington and a significant range extension to the north and west. *C. gracilis* is currently included on the Review Group 1 list in Washington (Washington Natural Heritage Program, 2004, List of plants tracked by the Washington Natural Heritage Program, Washington Natural Heritage Program, Washington Department of Natural Resources, Olympia, WA).

GALIUM PALUSTRE L. (RUBIACEAE).—Pend Oreille Co., Pend Oreille River, plants growing in locally wet area between Ruby boatlaunch and Le Clerc Road, with *Phalaris arundinacea*, *Carex vulpinoidea*, *Carex aperta*, *Symphotrichum laeve*. Plants are scrambling on other vegetation. Pressed specimens have turned black. 90° azimuth, 1% slope, 658 m elevation, T35N R44E S19 SW¼ of NE¼, 24 August 1996, Kathryn A. Beck & Florence E. Caplow 96062 (ALA). Specimens determined by D. Murray; Pend Oreille Co., sedge meadows along the Pend Oreille River, 1.7 km north of Usk, T33N R44E S30 SE¼, 650 m elevation, 10 August, 1998, sedge meadows along the west bank of the Pend Oreille River. C. Björk 3892.

Previous knowledge. *Galium palustre* is known from eastern North America, west to Ontario, Michigan and Montana, reported for Alberta and Manitoba, and introduced in the Yukon (Scoggan, 1979, The flora of Canada, National Museums of Canada, Ottawa, ON).

Significance. First documented collection in Washington.

HALIMOLOBOS PERPLEXA var. *PERPLEXA* (Henderson) Rollins (BRASSICACEAE).—Douglas Co., Sagebrush Flats, east of Moses Coulee, in open, vernal moist, thermally altered basalt gravel/scabland in shrub-steppe matrix with *Eriogonum douglasii*, *Lewisia rediviva*, *Penstemon gairdneri*, *Eriogonum thymoides*. 548 m elevation, T23N R25E S16, 28 May 2003, Florence E. Caplow 200302 (MO). Specimen determined by I. Al-Shehbaz.

Previous knowledge. This taxon was previously believed to be restricted to Adams and Idaho counties, Idaho.

Significance. This is the first collection from Washington, and represents a substantial disjunction to the west from the known range.

JUNCUS TIEHMII B. Ertter (JUNCACEAE).—Douglas Co., Moses Coulee, on flat, seepy bench area between two sloping areas above valley bottom. Natural seep in silt and clay accumulation on top of basal bedrock, with moss spp., *Epilobium minutum*, *Juncus bufonius*, *Agrostis interrupta*, *Poa secunda*, *Epilobium pygmaeus*, *Mimulus breviflorus*, 310° azimuth, 1% slope, 635 m elevation, T25N R25E S23, 5 June 1998, Kathryn A. Beck & Florence E. Caplow 98058 (WTU, UC). Specimens determined by B. Ertter. Same locality, 12 June 1998, Kathryn A. Beck & Florence E. Caplow 98065 (WTU).

Previous knowledge. This species was known from California, Oregon, Idaho, and Nevada.

Significance. This is the first collection from Washington, and represents a substantial range extension to the north. *Juncus tiehmii* is currently included on the Threatened list in Washington (Washington Natural Heritage Program 2004).

SCHIZACHYRIUM SCOPARIUM (Michx.) Nash var. *SCOPARIUM* (POACEAE).—Douglas Co., east bank of Columbia River below the Wells Dam, growing in cobbly, gravelly substrate in linear population at water's edge, with *Melilotus alba*, *Poa compressa*, *Sporobolus cryptandrus*, *Hypericum perforatum*, *Aristida purpurea*, *Solidago* sp. Plants are periodically inundated by river level fluctuations. 300° azimuth, 3% slope, 232 m elevation, T28N R23E S26, 27 May 1999, Kathryn A. Beck & Florence Caplow 99016 (WTU); Chelan Co., west bank of Columbia River below

the Wells Dam, growing in cobbly, gravelly substrate in linear population at water's edge, with *Aristida purpurea*, *Poa compressa*, *Juniperus scopulorum*, *Poa* sp., *Amelanchier alnifolia*, *Hypericum perforatum*. Plants are periodically inundated by river level fluctuations. 90° azimuth, 2% slope, 230 m elevation, T28N R23E S23, 15 July 1999, Kathryn A. Beck 99039 (WTU); Douglas Co., east bank of the Columbia River below Rocky Reach Dam. Plants growing below high water level in a discontinuous line in cobbly, gravelly substrate, with *Melilotus alba*, *Poa compressa*, *Dichanthelium acuminatum*, *Aristida purpurea*, *Grindelia columbiana*, *Heterotheca villosa*, *Asparagus officinalis*, *Lupinus lepidus*, *Lomatium grayi*, *Hypericum perforatum*. Population is at upper end of Rock Island Dam pool where the original (pre-dam) shoreline is unflooded, 270° azimuth, 3% slope, 197 m elevation, T23N R20E S15, 16 August 2001 Kathryn A. Beck 200134 (WTU).

Previous knowledge. *Schizachyrium scoparium* is present in almost all states in the continental United States. It is most prevalent in the central and southern Great Plains.

Significance. These collections represent the first documented collections from Washington. *S. scoparium* var. *scoparium* is currently included on the Threatened list in Washington (Washington Natural Heritage Program 2004). In 2000, this taxon was also seen in Stevens Co., Washington, in similar habitat along the upper Columbia River by Rex Crawford of the Washington Natural Heritage Program.

SISYRINCHIUM MONTANUM Greene var. *MONTANUM* (IRIDACEAE).—Douglas Co., Columbia River, Rocky Reach, north of Beebe Bridge, in mossy, vernal moist spring on side of hill at high water level of Columbia River in sandy silt loam, with *Pinus ponderosa*, *Juniperus scopulorum*, *Medicago sativa*, *Juncus balticus*, *Solidago canadensis*, *Asparagus officinalis*, *Artemisia ludoviciana*, *Hypericum perforatum*, 280° azimuth, 35% slope, 232 m elevation, T27N R23E S22, 26 May 1999, Kathryn A. Beck & Florence E. Caplow 99011 (WTU, MIN). Specimens determined by A. Cholewa.

Previous knowledge. This taxon ranges throughout the Rocky Mountain states, mostly east of the continental divide, north to British Columbia and Alberta and south to Texas (Henderson 1976).

Significance. This is the first record of this species in Washington. It represents a range extension of approximately 270 km to the west from the nearest known population in northern Idaho near the British Columbia border. *S. montanum* is currently included on the Threatened list in Washington (Washington Natural Heritage Program 2004).

SPIRANTHES DILUVIALIS Sheviak (ORCHIDACEAE).—Okanogan Co., saline marshes at the northern tip of Wanacut Lake. T39N R26E S11, 600 m elevation, 4 August, 1998; 4 miles SW of Oroville, 7 miles south of the International border. Associated species include *Juncus balticus* s.l., *Juncus torreyi*, *Eleocharis rostellata*, *Potentilla argentea*, *Carex viridula*. C. Björk 3508; Chelan Co., Columbia River near Beebe Bridge, in moist, herbaceous, weedy meadow, in dark loamy soil, near small pond, east side of Columbia River, with *Dichanthelium acuminatum*, *Poa compressa*, *Symphotrichum spathulatum*, *Melilotus alba*, *Coreopsis tinctoria* var. *atkinsoniana*, *Phalaris arundinacea*, *Equisetum* sp. 190° azimuth, 1% slope, 232

m elevation, T27N R23E S17, 21 July 2000, *Kathryn A. Beck and Florence E. Caplow 200017* (NYS). Specimens determined by C. Sheviak; Chelan Co., Columbia River, Rocky Reach, north of Beebe Bridge, in moist, herbaceous meadow adjacent Columbia River, with *Poa compressa*, *Agrostis* sp., *Plantago lanceolata*, *Solidago canadensis*, *Melilotus alba*, *Panicum occidentale*, *Equisetum* sp. Meadow inundated periodically by rising river levels. 135° azimuth, 2% slope, 232 m elevation, T28N R23E S35, 1 August 2000, *Kathryn A. Beck & Florence E. Caplow 200021* (WTU).

Previous knowledge. This species is known from southeastern Idaho, Montana, Utah, Colorado, Wyoming, Nebraska, and Nevada.

Significance. This globally rare species is new to Washington. These collections represent a range extension of approximately 600 km from the nearest populations in Montana. *S. diluvialis* is federally Threatened and is listed as Endangered in Washington (Washington Natural Heritage Program 2004).

—KATHRYN A. BECK, Beck Botanical Services, 1708 McKenzie Ave. Bellingham, WA 98225. calypso@openaccess.org; FLORENCE E. CAPLOW, Washington Natural Heritage Program, Department of Natural Resources, P.O. Box 47014, Olympia, WA 98504-7014; CURTIS R. BJORK, Stillinger Herbarium, University of Idaho, Moscow, ID 83843.

REVIEWS

Native Plants for High-Elevation Western Gardens. By JANICE BUSCO and NANCY R. MORIN. 2003. Fulcrum Publishing, Golden, Colorado. 352 pp. Paperback \$29.95. ISBN 1-55591-475-6.

"The textured patchwork of plant communities as they spread, merge, and change tells us the story of our home: where the water flows, where the soils are heavy, where the wind and sun conspire to parch the land, where we have disturbed the earth, where cows and sheep have fed, where elk have stood. When we use native plants in natural combinations, they link us even more closely to our sense of place."—Busco and Morin 2003

Few and far between are books written for landscaping and growing high elevation native gardens, and finally, here is a great one. Award-winning (Garden Globe Award of Achievement for Writing and a 2003 Southwestern Book of the Year), *Native Plants for High-Elevation Western Gardens* ably rises to the task.

Horticulturist, Jan Busco, elegantly and logically escorts her readership through the essential subjects: climate & its affects on plants and planting, consideration of conditions and available resources, site assessment, landscape plan preparation, planting and seeding techniques as well as monitoring plantings and keeping them well. These topics are succinctly and confidently addressed—clearly evidence of the author's many years of horticultural experience. The 'Plant Description' section describes 150 or so herbaceous perennial species in which character, native range, blooming season, outstanding features, culture, and interesting (really!) detailed comments about use or cultivation of each species. High quality color images illustrate every species, making this book not only a lovely work of art, but one useful for field identification.

While the epicenter for this book is Flagstaff, Arizona, where all of the cultural trials were performed, the information is truly applicable to all of the mountainous western states (4000'–12,000' elevations) in principal. And, while the species listed within the 'Plant Description' section might not be appropriate to introduce, for example, to the Sierra Nevada Mountains, in most cases, the cultural information provided for each genus, can be directly applied to help grow similar species native to other regions.

—MELANIE BAER-KEELEY, Restoration Horticulturist, Sequoia Kings Canyon National Parks, Three Rivers, CA 93271

Theodore Payne in His Own Words, a Voice for California Native Plants. Compiled and edited by ELIZABETH POMEROY. 2004. Many Moons Press, Pasadena, California. 224 pp. Paperback \$16.95. ISBN 0-9700481-5-7.

Theodore Payne arrived in southern California as a young man in the 1890's, having been recently trained in horticulture in his homeland, England. Early on in his career here, he recognized the uniqueness and fragility of California's native plants, making a lifelong commitment toward their protection and preservation. As a nurseryman, Payne grew and introduced 400–500 native species into gardens, becoming a noted expert at cultivating and propagating them. It is fortunate for us that he, so early on in southern California's history, recognized how profoundly altered the wildness of this state would become.

Theodore Payne in His Own Words, a Voice for California Native Plants is a compilation of his writings from primarily 1890–1940. He chronicles his explorations, experiences, observations and career path throughout southern California. Colorful characters parade through the pages of this book as they did in his life, and combined with Payne's orientation towards all things wild—especially plants—makes for very interesting reading. Having a glimpse of southern California as it was before the deluge of people and development is a rewarding, uncommon treat.

What also makes this book really interesting is Payne's involvement with prominent botanists, horticulturists, and landscape architects of the day, along with details of several renowned projects. His associates are a veritable 'Who's Who' in his profession, such as Frederick Law Olmstead, Ralph Cornell, Hugh Evans, Kate Sessions, Susanna Bixby Bryant, Dr. Carl Wolfe, and Dr. Francesco Franceschi. Payne's influence on these people and others ultimately promoted further efforts toward conservation and education. For example, Theodore Payne inspired, designed, as well as propagated plants for two of the premier California native plant botanic gardens and research facilities—Santa Barbara Botanic Garden and Rancho Santa Ana Botanic Garden. And several of Payne's other native landscapes—which he also designed and grew plants for—include Exposition Park, Cal Tech, and Descanso Gardens, Torrey Pines State Park, Pomona and Occidental College. His private landscapes were scattered widely through the San Fernando Valley in Pasadena, Hollywood and Beverly

Hills, and north to Ojai and Santa Barbara. Vestiges of many of Payne's original plantings still remain.

In his lifetime, Theodore Payne clearly demonstrated his commitment to "... promote, preserve and restore California native landscapes and habitats," as well as in a lifetime beyond with the establishment in 1960, of the Theodore Payne Foundation for Wildflowers and Native Plants. The publication of *Theodore Payne in His Own Words, a Voice for California Native Plants*, rightfully reminds and acknowledges such a deep and worthy dedication.

—MELANIE BAER-KEELEY, Restoration Horticulturist, Sequoia Kings Canyon National Parks, Three Rivers, CA 93271

California desert flowers: an introduction to families, genera, and species. By SIA MORHARDT and EMIL MORHARDT. 2004. University of California Press, Berkeley, CA. 284 pp. Hardcover \$65.00, Paperback \$29.95. ISBN 0-520-24003-0.

This wonderful book provides a great introduction to the desert flora of California for beginning botanists, and will be a useful tool for exposing nontraditional students to scientific classification and taxonomic keys. More experienced students of California's flora will also value this book as a complement to more technical works (Munz 1974; Hickman 1993). The layout and content are well chosen, and will interest a wide readership.

As the book is very photograph-driven, the coverage is primarily of the showiest species from twenty-four families found in the Mojavean and Sonoran regions. These photographs are outstanding, even breathtaking in places. Although the stated purpose of introducing California's desert flora is performed very well, these photographs clearly reveal the book's metafunction: an emotive tribute to the authors' very deep respect of our state's tremendous beauty. This duality makes for a very engrossing read: close shots of choice blossoms seduce the reader as they admirably illustrate diagnostic features. Other photographs carefully capture the unique landscapes of the region with genuine sensitivity—the images of long views across dry bolsons (e.g., *Eucnide urens*, p. 188), scorched silver playas (*Lupinus magnificus*, p. 146), and cloud-shaded paintbrushed plains (*Escholtzia californica*, p. 220) will resonate deeply with many readers.

The photographs are complemented by useful diagrammatic icons and illustrations which demonstrate diagnostic features. All of these appeared accurate as of my first read, with the (minor) exception of a palmately lobed leaf labeled as a palmately

compound leaf (p. 9). Additionally, well-written taxonomic keys lead the reader to the taxa treated in the book, either genera or species.

Some subtle editorial content provides levity, but shows a measure of internal dissonance: Broccoli is mentioned as "the vegetable that George Bush I refused to eat (p. 107)," whereas later, the authors echo similar distaste for okra (p. 202). Elsewhere, use of the phrase "more favorable circumstances (p. 1)" to describe non-desert regions continues the traditional depiction of deserts as somehow impoverished, inferior or more hostile relative to non-desert regions (cf. 'cismontane' and 'transmontane' California, two geographically biased terms); although this may be true for many species (including some humans), 'favorable' and 'unfavorable' are relative terms, dependent on each individual. As this is a book of desert-adapted flora, many of the plants depicted here are growing under the most favorable conditions possible. The authors are entitled to these opinions, however.

The book deserves praise for presenting very accurate diagnostic information in an accessible format, and for also presenting much other interesting and useful content, including ethnobotany, nomenclature, and ecology. One novel portion concerns the etymology of *Opuntia*, which the authors suggest may have come from the Tohono O'odham word for prickly pear fruits ("opun," p. 116); other authors maintain this taxon (adopted by Tournefort by 1700, authored by Linnaeus in 1753, but most often used *sensu* Miller, 1754) is traced from ancient works of Theophrastus and Pliny the Elder, both of whom mention a plant growing near Opus (Greece), called *opuntia*, which can 'sprout roots from the leaves' (Crook and Mottram 1995).

I have seen this book used by non-botanists to identify wildflowers to genus, and their opinion was very favorable. The Morhardts have produced a welcome addition for anyone interested in natural history of California, and one especially important for beginning botanists; professional botanists will welcome it as well.

—M. PATRICK GRIFFITH, Department of Botany, Claremont Graduate University; Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, California. michael.patrick.griffith@cgu.edu

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Fire, chaparral, and survival in southern California. Richard W. Halsey, editor and author. 2005. Sunbelt Publications, San Diego, CA. ISBN 0-932653-69-3. \$19.95.

Mother Nature has lavished many gifts on California, but she has made mistakes. Some were easily corrected. Grizzly bears were too fierce and unpredictable, but they trouble Californians no longer. Water was poorly distributed, but it now flows freely into the semi-arid southern counties. Other imperfections of the California environment have resisted easy correction. Two in particular continue to bedevil the state—earthquakes and fire. As is pointed out in the volume under review, the popular response to these two challenges has been strikingly different. Few expect the earthquake problem to be solved any time soon. It is understood that if you want to live in the land where the lemon tree flowers and the laurel sumac perfumes the air you must run the risk of being buried under a collapsing building. The public accepts the costs of the precautions which reduce risk, and they also accept that although the risk is small, it's there and nothing can make it zero.

Like earthquakes, fires are a recurrent phenomenon in California that shows no signs of going the way of the grizzly bear. On the contrary, as measured by damage to life and property, the wildland fire situation seems to be getting worse. One might therefore expect that people would accept it as a fact of life, pay the costs necessary to reduce its impact, and adjust their affairs accordingly. In the opinion of Halsey (chief author and editor) and probably most of the contributing authors of this volume, the contrary is true. The public seems to view fire not as an act of God, but as the act of fools and criminals—a bad thing which has happened to them because of the incompetence or negligence of others.

It is the premise of this volume that this attitude must be changed if we are to find a workable solution to the chaparral fire problem, and that education is the key. Halsey clearly believes that if people only understood how the natural system works and came to respect it, they would see the way to deal with fire. This puts him firmly into the camp of those who think the fire problem is not a fire problem, but a people problem.

A notable achievement of the author/editor was to have moved the book from conception to publication in a very short time after the 2003 fires. Halsey accomplished this by writing much of the text himself, but also soliciting contributions for others and gluing these together with introductory remarks and bridging commentary. The timely appearance is commendable and significant. Anyone who has lived through past fire disasters knows that the sharp spike in public interest immediately after a disaster drops faster than a *Phacelia brachyloba* population. There is the disaster-awareness equivalent of the "teachable moment".

The book is grouped into eight chapters with a total of 16 authors (including the author/editor). Another six persons made other contributions. There are indeed, as the author states "many voices in this book". As the title indicates, the book focuses on southern California, and therefore on the brush-woodland systems that are the main vegetation associated with the fire problem. Montane forest types are only touched on lightly, as is appropriate.

The most important parts of the book are those that expose the weaknesses in the simplistic thinking behind the "kick butt and take names" approach to reforming wildlands management—the approach that calls for mass firings in government agencies, or burning everything on

a 5 year rotation (but not hiring any new people to do it), or clearing all vegetation to mineral soil for 500 ft into adjacent publicly owned areas (but not requiring any removal of eucalyptus or pines in their own landscaping), or doubling the number of pilots and fire-fighting planes (but not increasing taxes). Such views assume that a naturally friendly system has been mismanaged to become a menace. But what does science tell us? Contributions of Keeley and Fotheringham and Moritz, as representatives of the science community, cast very serious doubt on this assumption. Keeley and Fotheringham present historical data that show that fire size is either getting smaller or staying roughly the same. If there is mismanagement, it hasn't manifested itself by making burns significantly larger. But what *has* definitely changed is the human population, which has increased by a factor of 30 over the last century. How can anyone doubt that this huge increase has something to do with our present dilemma, in which people and fire seem to intersect more often and more disastrously than they did in the past? From this follows one of the main points emphasized in the book—that the intrusion of poorly planned developments into wildlands is a major part of the problem. What is frustrating is that everyone knows this, but little is being done about it.

Moritz, who has made interesting contributions to our understanding of fire as a stochastic process, stresses the importance of concentrating our hazard reduction efforts in the places where they will have the most effect. This idea is not new¹, but it deserves to be stated again—as it is in several other places in the book. The resistance to the work-the-edges concept can be compared to the widespread refusal to grasp the realities of global climate change. Research scientists who are familiar with shrubland fire problems are near unanimous in advocating this approach, but because the message is not what people want to hear, and because in the short run they see no consequences of inaction, they refuse to listen. This fact justifies the premise of this book.

Managers of wildlands adjacent to urban areas are on the front lines of the struggle to deal with chaparral fire, and are in the best situation to tell us what works in practice. This makes the contribution of Witter and Taylor, relating the programs at the Santa Monica Mountains of particular importance. Wildland islands in an urban sea are now cut off from regional fires, but simultaneously are susceptible to arson and accidental ignition. Thus, a laissez-faire approach to fire is not an option. Although complete fire exclusion would in the long run be bad for the

¹ The publication *Proceedings of the Symposium on Living with the Chaparral* 1974. C. Rosenthal Conference Chairman, and M. Rosenthal, Editor, Sierra Club, San Francisco, CA, is one example. Larry Moss (Sierra Club) wrote: "Our greatest problem is, of course, the development of housing patterns that reflect little understanding or respect for the needs of chaparral." J. Zivnuska (University of California) "... it becomes clear that there are three main ways [of minimizing the costs of damage from fires] ... 1) changes in the locations in which structures are built and people live; 2) changes in the nature of the facilities constructed; and 3) changes in the relationships of fuels to structures. P. Zedler wrote: "... the wise use of chaparral resources [requires] the placement of human developments in locations where they will not be endangered every time [there is a wildfire]". Thirty years later we are still trying to get this message across.

vegetation, this is a purely hypothetical problem—the arsonists will make sure of that. The real threat to the Santa Monica Mountains is too much fire. The authors make their points with restraint, but one deserves to be restated in a stronger form: The fuels-based “mosaic model” based on management burns across the entire landscape and the great hope of the previous century, has been a complete failure. The plan that has been adopted in the Santa Monica Mountains is based on strategic hazard reduction targeted to specific areas where it is most likely to make a difference.

A good portion of the book is taken up by contributions from practitioners, agency staff, and interested citizens. Collectively these are a good feature of the book and a source of hope. Thoughtful research scientists understand that their data-based pontifications can only provide a background to better solutions. Action-based programs must enlist the energies and imagination of all of us. Several contributions show, from different angles, how it is possible to think and act differently. Klaus Radtke, a veteran of many fires and a survivor of many meetings about what to do about them, provides particularly useful and relevant information. He explains how he and his wife dealt with the hazards that they faced living on the wildland boundary. His story is anecdotal, but it points the way to the kinds of management actions and education programs that are needed. As Halsey asserts, mass panic and the mandatory evacuation of neighborhoods are not inevitable if there is prior planning and if citizens accept some responsibility for their own protection, as Radtke and his wife did. In another chapter, Radtke also provides useful advice on erosion control and pre-fire planning. In this section he adds his voice to the long list of experts who condemn the broad scale seeding of exotic grasses as a post-fire erosion control measure. But his is not a purist approach. He advocates seeding barley in small areas in a strategic manner, an example of how targeted efforts can achieve much better results with far less damage to the natural regeneration capacity of the chaparral system.

The inclusion of the views of fire fighters is another commendable feature. Although some might object to the “literary” approach—the attitudes and ideas are said to be factual, but it is conveyed as a fictional narrative—these sections help us to visualize the fire problem from the point of view of those taking the greatest risks to deal with it. It helps us to understand their frustrations with lack of understanding of fires and unrealistic expectations of the public for fire suppression and control. Further, no one will doubt that a workable solution must have the buy-in of the fire-fighting agencies.

The book begins with a mini-course in chaparral ecology. The author's intent is to provide a basic introduction to chaparral ecology to a general reader so that they can understand why fires occur and how vegetation responds. I applaud the objective, but there are a few problems. The reader needs to be cautioned that some of the terminology is idiosyncratic and a few facts seem at least disputable. Some examples: The etymology of chaparral is discussed (does it need to be?) with the dubious conclusion that chaparral is the anglicized form of *chapparro*. But, so a colleague in Barcelona tells me, the Academia Real says that *chaparral* is a perfectly good Spanish word—with a derivation from its root similar to *matorral* from *mata*. Halsey says that in Arizona they have only “mock chaparral”. But they have scrub oaks, and so why not chaparral? I would expect brush loving “Zonies to take offense. Contrary to what is implied, all chamise seeds do not re-

quire a high temperature treatment to germinate. “Type conversion” is not best defined as “the process by which one type of plant community replaces another”. Although there are plenty of anecdotes about Native Americans using fire, it goes beyond the data to say that they “regularly burned the chaparral” and that a main purpose was to “reduce grizzly bear contact” (though it is understandable that they might like to do so). If the coastal sage scrub remains open “allowing for the continual recruitment of seedlings” how is it that it can stay open? Why are sclerophyllous leaves a “drought avoidance” adaptation, but closing of stomates an adaptation for “persistence”? Is “chameleon” a good term for those shrubs that (also incorrectly in my view) have been said to have “dimorphic leaves”? Describing *Artemesia californica* “establishing seedlings after fire” could mislead readers to think that they do not do so at other times.

In a section titled “chaparral mythology” the author devotes considerable space to allelopathy. While this is an interesting topic, it doesn't seem especially relevant to the fire problem. Likewise, although I am an ephemeralophilic myself, I am not sure that information on vernal pools is especially important for understanding fire. Given these sections it is surprising that coastal sage scrub is treated only very briefly. The author is on target, however, in his discussion of the concept of “senescence”. According to popular belief and the opinion (but not so much the data) of some researchers, chaparral rapidly deteriorates with time, accumulating dangerous fuels. Hence the need for short rotation times between fires. But when the age-dead fuel relation has been tested with data, it has been found to be weak to non-existent. If we are going to treat “senescent” chaparral to keep it healthy, we had better move on to the desert, where “senescent” creosote bushes typically have many dead stems. Before we do this, however, we may want to think about the fact that creosote bush clones have been shown to be hundreds or even thousands of years old despite fire being rare to non-existent. Dead branches do not necessarily predict imminent demise.

There is a photographic section which includes mostly good pictures of 64 “essential” chaparral plants, although a number are really more characteristic of the coastal sage scrub. This is aimed at the beginner, and although other flower guides and books would have similar information, a case can be made for including them here to give the general reader a better idea about the organisms discussed in the text.

I found myself agreeing with the general conclusions that emerge collectively from the contributions and Halsey's editorializing. Not everyone will. Fuels-based solutions receive a pretty thorough drubbing in this book, and there are certain to be some who consider the book to be unbalanced. I think it probably is, but given the years of propaganda from the other side I think this is justified. Here we see the case made for the view that chaparral fires are primarily weather-controlled and therefore they cannot be eliminated by fiddling with fuels. Of course attention must be paid to fuels, but chamise bushes innocently doing their best to control erosion out in the large patches of native vegetation are not the main problem. The fuels to worry most about are those in our houses, landscaping, and yes, the native vegetation closest to what we wish to protect. Those who believe in the “fuel accumulation” theory will probably be OK with the “work the edges” idea, and will also agree that patterns of development should be more sensitive to fire risks. But they will probably not agree with the overall explanation for why we have a problem. Yet for much of what most ur-

gently needs to be done, the difference among the so-called experts is irrelevant. The problem arises more with respect to long-term strategies. If you think that creating an age mosaic that conforms to a presumed historical pattern will solve the problem, you will be in favor of a long-term strategy markedly different from another person who thinks that such a scheme will accomplish nothing. This book will not settle the controversy, but by presenting in one place a vigorous argument against a simplistic fuels-based explanation along with practical advice and per-

spectives from a variety of people who deal directly with fire and its consequences, it provides a valuable service. I can recommend the book to anyone who wants to understand the fire situation in California, but with the cautions given above.

—PAUL H. ZEDLER, Nelson Institute for Environmental Studies and UW Arboretum, University of Wisconsin–Madison, 550 N. Park St., Madison, WI 53706. phzedler@wisc.edu

ANNOUNCEMENTS

THE RUPERT BARNEBY AWARD

The New York Botanical Garden is pleased to announce that Vidal de Freitas Mansano, of the Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, and Benjamin M. Torke, currently a graduate student in the Department of Biology, Washington University, St. Louis, are the joint recipients of the **Rupert Barneby Award** for the year 2005. They will be studying the systematics and diversification of *Swartzia* (Leguminosae, Papilionoideae, Swartzieae), a prominent neotropical tree genus of approximately 140–180 species, with species diversity concentrated in lowland rainforests of the Guianas and Amazonia.

The New York Botanical Garden now invites applications for the **Rupert Barneby Award** for the year 2006. The award of U.S. \$1000.00 is to assist researchers to visit The New York Botanical Garden to study the rich collection of Leguminosae. Anyone interested in applying for the award should submit their curriculum vitae, a detailed letter describing the project for which the award is sought, and the names of 2–3 referees. Travel to the NYBG should be planned for sometime in the year 2006. The application should be addressed to Dr. James L. Luteyn, Institute of Systematic Botany, The New York Botanical Garden, 200th Street and Kazimiroff Blvd., Bronx, NY 10458-5126 USA, and received no later than December 1, 2005. Announcement of the recipient will be made by December 15th.

Anyone interested in making a contribution to **THE RUPERT BARNEBY FUND IN LEGUME SYSTEMATICS**, which supports this award, may send their check, payable to The New York Botanical Garden, to Dr. Luteyn.

ANNETTA CARTER MEMORIAL FUND
OF THE CALIFORNIA BOTANICAL SOCIETY
APPLICATION NOTICE AND GUIDELINES FOR 2005
GRANT PROPOSALS

The Annetta Carter Memorial Fund honors Annetta Carter, who devoted the last 40 years of her life to the study of the Baja California flora. Her special interests were floristics, history, biogeography, and ethnobotany of the Sierra de la Giganta.

The review committee will consider proposals from members of the California Botanical Society who are conducting or proposing to conduct botanical research on the green plants of Baja California.

Studies of populations outside Baja will also be considered if they elucidate problems in Baja California.

Funds may be requested for research, travel, supplies, and minor equipment. Requests for major equipment ($\geq \$500$) will not be considered. Projects should be designed to result in a professional publication in a scholarly journal, preferably Madroño. The proposed budget should not exceed \$1000 and applicants are encouraged to prioritize budget items as only partial funding may be available.

To apply, send a resume and 1–2 page description of the goals, methods, and significance of the proposed project. Proposals should also include a budget and budget justification that details what the grant funds will be used for. Applicants should also provide evidence that required permits will be obtained before the grant is awarded.

Requests for travel funding should adhere to the following guidelines: (1) land transportation in private vehicles should be stated in mileage, using the rate of \$0.36/mile, and (2) while in Baja, a maximum per diem of \$100 for lodging and \$50 for food will be awarded. For travel within the U.S., estimates for actual expenses should be made (meal allowance may not exceed \$50/day).

Previous recipients of Annetta Carter Fund awards should include an additional brief (one page or less) summary of work accomplished with prior support. Progress on previously funded research and evidence of effort to seek external funding will be considered favorably in review of proposals.

Recipients of grants should acknowledge the Annetta Carter Memorial Fund of the California Botanical Society in any publications that resulted from research, travel, or equipment supported by the grant.

Please address any questions regarding the Annetta Carter Memorial Fund to the Committee Chair, Staci Markos, Jepson Herbarium, 1001 VLSB #2465, Berkeley, CA, 94720.

Mail applications to:

California Botanical Society
Attn: Annetta Carter Memorial Fund
% University and Jepson Herbaria
1001 VLSB #2465,
Berkeley, CA 94720

Deadline for receipt for applications is October 15, 2005. Proposals will be peer reviewed and award letters will be sent by December 31, 2005.

FONDO MEMORIAL ANNETTA CARTER DE LA
SOCIEDAD BOTÁNICA DE CALIFORNIA
APERTURA DE CONVOCATORIA Y REQUISITOS PARA
BECAS 2005

El Fondo Memorial Annetta Carter conmemora a la Sra. Annetta Carter, quien dedicó los últimos 40 años de su vida al estudio de la flora de Baja California. Sus principales intereses fueron la florística, historia, biogeografía y la etnobotánica de la Sierra de la Giganta.

El comité evaluador considerará propuestas de miembros de la Sociedad Botánica de California que estén desarrollando investigaciones o que propongan desarrollar investigaciones en plantas verdes de Baja California. Estudios de poblaciones fuera de Baja también serán considerados siempre y cuando incluyan problemas relacionados con Baja California.

Se prodrá solicitar fondos para investigación, viáticos y equipo de bajo costo. No se considerará apoyo para equipo con un costo mayor de \$500.00. Los proyectos deberán ser diseñados de forma tal que los resultados sean publicados en revistas científicas, preferiblemente la Revista Madroño. El costo total de la propuesta no deberá exceder de los \$1000.00 y se le solicita a los aplicantes que maximizen los costos, ya que solamente se cuenta con fondos parciales.

Para aplicar, madar su hoja de vida, y de 1-2 páginas de descripción de los objetivos, métodos y racionalización del proyecto. Las propuestas también deberán incluir un presupuesto y una justificación del presupuesto, que describa en detalle como se utilizarán los fondos. Los aplicantes también deberán proporcionar evidencia de que todos los permisos requeridos para el proyecto serán conseguidos antes de que la beca sea otorgada.

Las solicitudes para los presupuestos de viáticos deberán seguir el siguiente formato: (1) Transporte por tierra, en vehículo privado, deberá ser escrito en millas, usando la proporción de \$0.36/milla, y (2) si se encuentra en Baja, se considerará un costo máximo por día de \$100.00 por hotel y \$50.00 por comida. Para viajes dentro de los Estados Unidos, se deberá someter un estimado de los costos (costo por comida no deberá exceder de los \$50.00 /día).

Aquellas personas que ya hallan recibido la beca Annetta Carter anteriormente deberán incluir un resumen adicional (una página o menos) que detalle los logros ya obtenidos. Cualquier progreso en las propuestas que han sido anteriormente financiadas y evidencia de que han

buscado fondos externos serán considerados como puntos favorables en el proceso de revisión de las propuestas.

Las personas que reciban la beca deberán agradecer al Fondo Memorial Annetta Carter de la Sociedad Botánica de California en cualquier publicación que resulte de las investigaciones, viáticos y equipos financiados por dicha beca.

Cualquiera pregunta o duda, por favor comunicarse con Staci Markos, Directora del Fondo Memorial Annetta Carter, Jepson Herbarium, 1001 VLSB #2465, Berkeley, CA 94720.

Enviar aplicaciones a la siguiente dirección:

California Botanical Society
Attn: Annetta Carter Memorial Fund
% University and Jepson Herbaria
1001 VLSB #2465
Berkeley, CA 94720

Fecha límite de entrega de documentos: 15 de Octubre, 2005.

Las propuestas serán evaluadas por científicos especialistas en el área (peer reviewed) y las cartas de aceptación serán mandadas el 31 de Diciembre de 2005.

THE OREGON PLANT ATLAS

The Oregon Flora Project announces the launching of the Oregon Plant Atlas, the first comprehensive on-line mapping tool for Oregon plants. Over 385,000 data points representing 4,337 taxa are derived from the Atlas specimen and observation databases, and virtually all information associated with each data point is accessible to the user by clicking on the dots. Information is continuously updated through the efforts of avid field workers and Oregon Flora Project staff. The Oregon Plant Atlas can be accessed through the Oregon Flora Project website at www.oregonflora.org. The Atlas is partially funded by National Science Foundation grant BRC-0237459, and by donations from individuals and plant-oriented societies including the Native Plant Society of Oregon.

MEMORIAL

IN MEMORIAM: SCOTT SUNDBERG, 1954–2004

Scott D. Sundberg of Corvallis, Oregon, died 30 December 2004 of cancer. An Oregon native, Scott's interest in the plants of the state began as an undergraduate at the University of Oregon. He was a botanist for the Bureau of Land Management, Coos Bay District from 1978–1980. He received his Ph.D. in botany in 1986 from the University of Texas at Austin, where he studied the taxonomy of plants within the Compositae. After post-doctoral studies in Ohio, and several years of research and botanical consulting in Seattle, Scott returned to Oregon to oversee the integration of the University of Oregon and the Oregon State University Herbaria.

In 1994, Scott initiated the Oregon Flora Project, with the goal of writing a new flora of Oregon. He

served as director for that project until his death, supervising over 60 students, several professional employees, and directing over 230 volunteers. Along with a new flora was his vision for and the establishment of the Oregon Plant Atlas, the Oregon Vascular Plant Checklist, the Oregon Flora Photo Gallery, and the *Oregon Flora Newsletter*.

Scott's 29 scientific publications include taxonomic papers, laboratory-based investigations in plant systematics, and treatments for checklists, field guides, and floras. The majority of his publications concern the composite family. A complete list of his scientific publications will appear in the *Oregon Flora Newsletter*.

Memorial gifts in Scott's honor can be made to NPSO–Oregon Flora Project, and mailed to P.O. Box 402, Corvallis, OR 97339.

SUBSCRIPTIONS—MEMBERSHIP

Membership in the California Botanical Society is open to individuals (\$27 per year; family \$30 per year; emeritus \$17 per year; students \$17 per year for a maximum of 7 years). Late fees may be assessed. Members of the Society receive *MADROÑO* free. Institutional subscriptions to *MADROÑO* are available (\$60). Membership is based on a calendar year only. Life memberships are \$540. Applications for membership (including dues), orders for subscriptions, and renewal payments should be sent to the Treasurer. Requests and rates for back issues, changes of address, and undelivered copies of *MADROÑO* should be sent to the Corresponding Secretary.

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Manuscripts submitted for publication in *MADROÑO* should be sent to the editor. It is preferred that all authors be members of the California Botanical Society. Manuscripts by authors having outstanding page charges will not be sent for review.

Manuscripts may be submitted in English or Spanish. English-language manuscripts dealing with taxa or topics of Latin America and Spanish-language manuscripts must have a Spanish RESUMEN and an English ABSTRACT.

Manuscripts and review copies of illustrations must be submitted in triplicate for all articles and short items (NOTES, NOTEWORTHY COLLECTIONS, POINTS OF VIEW, etc.). Follow the format used in recent issues for the type of item submitted. Allow ample margins all around. Manuscripts **MUST BE DOUBLE-SPACED THROUGHOUT**. For articles this includes title (all caps, centered), author names (all caps, centered), addresses (caps and lower case, centered), abstract and resumen, five key words or phrases, text, acknowledgments, literature cited, tables (caption on same page), and figure captions (grouped as consecutive paragraphs on one page). Order parts in the sequence listed, ending with figures. Each page should have a running header that includes the name(s) of the author(s), a shortened title, and the page number. Do not use a separate cover page or 'erasable' paper. Avoid footnotes except to indicate address changes. Abbreviations should be used sparingly and only standard abbreviations will be accepted. Table and figure captions should contain all information relevant to information presented. All measurements and elevations should be in metric units, except specimen citations, which may include English or metric measurements. Authors are encouraged to include the names, addresses, and e-mail addresses of two to four potential reviewers with their submitted manuscript.

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Line copy illustrations should be clean and legible, proportioned to the *MADROÑO* page. Scales should be included in figures, as should explanation of symbols, including graph coordinates. Symbols smaller than 1 mm after reduction are not acceptable. Maps must include a scale and latitude and longitude or UTM references. In no case should original illustrations be sent prior to the acceptance of a manuscript. Illustrations should be sent flat. No illustrations larger than 27 × 43 cm will be accepted.

Presentation of nomenclatural matter (accepted names, synonyms, typification) should follow the format used by Sivinski, Robert C., in *MADROÑO* 41(4), 1994. Institutional abbreviations in specimen citations should follow Holmgren, Keuken, and Schofield, *Index Herbariorum*, 8th ed. Names of authors of scientific names should be abbreviated according to Brummitt and Powell, *Authors of Plant Names* (1992) and, if not included in this index, spelled out in full. Titles of all periodicals, serials, and books should be given in full. Books should include the place and date of publication, publisher, and edition, if other than the first.

All members of the California Botanical Society are allotted 5 free pages per volume in *MADROÑO*. Joint authors may split the full page number. Beyond that number of pages a required editorial fee of \$40 per page will be assessed. The purpose of this fee is not to pay directly for the costs of publishing any particular paper, but rather to allow the Society to continue publishing *MADROÑO* on a reasonable schedule, with equity among all members for access to its pages. Printer's fees for illustrations and typographically difficult material @ \$35 per page (if their sum exceeds 30 percent of the paper) and for author's changes after typesetting @ \$4.50 per line will be charged to authors.

At the time of submission, authors must provide information describing the extent to which data in the manuscript have been used in other papers that are published, in press, submitted, or soon to be submitted elsewhere.



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A WEST AMERICAN JOURNAL OF BOTANY



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Editor—DR. JOHN HUNTER
c/o UC Davis Herbarium/Center for Plant Diversity
Plant Biology
One Shields Avenue
University of California Davis
Davis, CA 95616
johnhunterca@sbcglobal.net

Book Editor—JON E. KEELEY
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Corresponding Secretary: Susan Bainbridge, Jepson Herbarium, University of California, Berkeley, CA 94720-2465, suebain@sscl.berkeley.edu.
Treasurer: Roy Buck, Jepson Herbarium, University of California, Berkeley, CA 94720-2465, fax: 1.510.643.5390, roybuck@email.msn.com.

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TWO LINEAGES OF *ARCTOSTAPHYLOS* (ERICACEAE) IDENTIFIED USING THE INTERNAL TRANSCRIBED SPACER (ITS) REGION OF THE NUCLEAR GENOME

LAURA M. BOYKIN^{1,2}, MICHAEL C. VASEY, V. THOMAS PARKER,
AND ROBERT PATTERSON

Department of Biology, San Francisco State University, San Francisco, CA 94132

ABSTRACT

The understanding of evolutionary relationships in *Arctostaphylos* has been hampered by taxonomic difficulties in this large and complex genus. A phylogenetic analysis of sequences from the ITS region for 38 species was used to provide a phylogenetic perspective for interpreting evolutionary patterns and relationships in *Arctostaphylos*. Phylogenetic relationships were estimated using maximum likelihood and Bayesian inference. ITS sequence data do not support a previously published subgeneric classification based on morphological characteristics, but do support the two lineages of *Arctostaphylos* described by a previous molecular phylogeny based on RFLP data. Topology tests indicate morphological characters are not useful in defining monophyletic clades.

Key Words: *Arctostaphylos*, California, Ericaceae, Arbutioideae, manzanita, polyploidy, hybridization, life history evolution.

One of six genera included in subfamily Arbutioideae (Hileman et al. 2001), *Arctostaphylos* (Ericaceae) is a taxonomically complex genus with over 100 taxa of evergreen shrubs and trees. The center of *Arctostaphylos* diversity is in the California Floristic Province (Raven and Axelrod 1978); only 8 taxa are found outside this province (Wells 2000). Over half of these species are considered rare, threatened or endangered by the California Native Plant Society. Species diversity is highest (over 30 species) along the coast of California from Mendocino County to San Luis Obispo County. Many of the species have limited distributions and are restricted to specific substrates such as serpentine and shale (Wells 1962; Gankin and Major 1964). In contrast, one widespread taxon, *A. uva-ursi*, has a circumboreal distribution and is common in Canada and the northern United States with a continuous distribution across Asia and Europe, occurring in coastal or high mountain areas farther south (e.g., the Alps and Caucasus Mountains in Eurasia or the Rocky Mountains in North America) (Packer and Denford 1974).

Diversification of *Arctostaphylos* has been attributed to life history changes in the context of a complex and changing ecological environment, especially the exposure of a diversity of soil types and the increase in fire frequencies in the last 1.5 MY (Stebbins and Major 1965; Stebbins 1974; Axelrod 1981). Two different life history patterns are found within the genus. In the first, plants survive wildfire and resprout (facultative sprouters). In the

second, plants are killed by fire (obligate seeders). In both cases, populations recover from persistent dormant seed banks that are stimulated by fire (Keeley and Zedler 1978; Parker and Kelly 1989). Obligate seeding has been proposed as facilitating the radiation of *Arctostaphylos* into different soil and habitat types (Wells 1969; Stebbins 1974; Raven and Axelrod 1978).

Polyploidy and diploid hybridization (Gottlieb 1968; Stebbins 1974; Kruckeberg 1977; Roof 1978; Schierenbeck et al. 1992) are considered to be major evolutionary processes involved in the rapid speciation in the genus (Stebbins and Major 1980). The base chromosome number for *Arctostaphylos* is $x = 13$ (Wells 1968) and the genus contains both diploids ($n = 13$) and tetraploids ($n = 26$); (Wells 1992). Evidence for allopolyploidy has been found for the origin of at least two taxa (Schierenbeck et al. 1992). Interspecific hybridization has been documented for *Arctostaphylos*, where two compatible species have overlapping distributions and come into close enough contact for cross-pollination (Dobzhansky 1953; Gottlieb 1968; Schmid et al. 1968); diploid hybridization has been suggested as the origin of several species (Gankin 1967; Parker and Vasey 2004). Although hybridization exists, it is not pervasive enough to result in the breakdown of species boundaries (Dobzhansky 1953; Gottlieb 1968; Keeley 1976; Kruckeberg 1977).

A combination of vegetative diversification in *Arctostaphylos* with little divergence in floral characters has led to varying taxonomic interpretations (Jepson 1922, 1939; Eastwood 1934, 1937; Mc-Minn 1939; Adams 1940; Wells 1987, 1992, 2000). Recently, Wells (1992, 2000) provided the most comprehensive and hierarchical treatment. Wells (1992, 2000) divided the genus into two subgenera

¹ Present address: USDA, ARS, USHRL, 2001 South Rock Road, Fort Pierce, FL 34945

² Author for correspondence, email: lboykin@ushrl.ars.usda.gov

based on fruit characteristics: *Micrococcus* (pulpless, cylindroid, somewhat achene-like drupe with 2–5 separable nutlets) and *Arctostaphylos* (subglobose, berry-like drupes with mealy, granular mesocarp and/or thick leathery pericarp, nutlets 8–10, separable, or partially or fully fused). Subgenus *Micrococcus* was divided into three sections, *Myrtifolia*, *Nissenana*, and *Micrococcus* based on several morphological features of the flower, floral bracts, leaves and bark. Using features of inflorescence bracts, Wells also further divided subgenus *Arctostaphylos* into three sections: *Arctostaphylos*, *Foliobracteata*, and *Pictobracteata*. The sections were further subdivided into subsections based on presence of basal burl, stomatal distribution and other morphological characters.

Recent systematic research on the Arbutioideae (Hileman et al. 2001) and *Arctostaphylos* (Markos et al. 1998) has underscored the value of using molecular data to evaluate phylogenetic relationships and to test the previous morphology-based classifications. Hileman et al. (2001) used nuclear ribosomal sequence data to study the phylogenetic relationships of the six genera of Arbutioideae: *Arbutus*, *Arctostaphylos*, *Arctous*, *Comarostaphylis*, *Ornithostaphylos*, and *Xylococcus*. *Arctostaphylos* was determined to be one of the more recently derived genera in this group. Markos et al. (1998) were the first to use molecular data in phylogenetic research within *Arctostaphylos*. The nuclear ribosomal Internal Transcribed Spacer (ITS) region was sequenced for a small group of nine taxa (five of which were subspecies of *A. hookeri*) that indicated two clades in the genus. This was tested with sequences from a portion of the 26S nuclear ribosomal DNA of 17 species. These data indicated two clusters of species that conflicted with Wells' classification; while there seemed to be a deep split between the two clusters, there was no further resolution. Restriction fragment data derived from the nuclear ribosomal ITS region were then used to test Wells' 1992 subgeneric classification of *Arctostaphylos*, examining 34 species in the genus. The recognition of Wells' two subgenera in the genus was not supported although Markos et al. (1998) did consistently find two different but distinctly supported groups ("Group one" and "Group two") in each analysis.

The goal of the present study is to assess phylogenetic relationships within *Arctostaphylos* using ITS sequence data. We have extended the taxa sequenced for ITS in the genus beyond that of Markos et al. (1998) from 9 to 38 taxa. The phylogenetic hypotheses generated using the molecular data are used to address these specific questions:

1. Does the ITS phylogeny support the infrageneric classification proposed by Wells (1992) or the two groups recognized by Markos et al. (1998)?
2. Will traditionally used morphological characters, such as shreddy bark, unequal stomata, bract

type, and chromosome number support monophyletic clades found in the molecular phylogeny?

MATERIALS AND METHODS

Taxa and Regions Sampled

Thirty-eight species of *Arctostaphylos* were included in this study (Table 1). Sequence data were deposited in TreeBASE (accession number SN1430) and Genbank (Table 1). Markos et al. (1998) indicated that the lack of intraspecific variation in the ITS region precluded the need for inclusion of more than one individual per species in the study. This was supported in another study of wide-ranging diploid species of *Arctostaphylos*; no variation in ITS sequence was found from geographically widespread individuals in three species, while in another species, one individual differed by 1 base pair from 4 others (Parker et al. unpublished data). For this reason, only one individual per taxon was sampled in this study. Sampling was designed to include taxa from the two subgenera and three sections described by Wells (1992). *Arbutus* was used as the outgroup based on the results of Hileman et al. (2001).

DNA Extraction, Amplification, and Sequencing

Total DNA was isolated from dried leaves of individual plants. DNA extraction followed a modified Doyle and Doyle (1987) CTAB extraction (Cullings and Bruns 1992). Double-stranded PCR products were amplified using the universal primers ITS4 and ITS5 (White et al. 1990). The 50- μ l PCR reactions were heated at 94°C for three minutes. The reactions underwent 35 cycles in a Perkin-Elmer 480 thermocycler. Each cycle consisted of 35 sec at 97°C denaturation, 45 sec at 50°C annealing and 1 min 15 sec at 72°C extension. Prior to sequencing, the amplified products were cleaned using a PEG precipitation method (Kusukawa 1990).

Amplification primers were used for sequencing. All sequencing was done using dye primer sequencing on a Catalyst 800 Molecular Biology Lab Station following the protocol specified by the ABI PRISM[®] Dye Primer Cycle Sequencing Ready Reaction Kit (Revision B, August 1995, Perkin-Elmer). Sequence fragments were assembled with Sequencher[®] version 3 (Gene Code Corporation, Ann Arbor, MI) and then visually inspected.

Molecular Data Analyses

Skewness of distribution of tree length was tested using the methods described by Huelsenbeck (1991). Evaluating 20,000 random trees using PAUP* (Swofford 2003) generated a g_1 skewness statistic that assessed the non-randomness of the data set. Base frequencies were also calculated using PAUP*. Base composition bias was calculated according to Irwin et al. (1991).

TABLE 1. COLLECTIONS EXAMINED IN THE PHYLOGENETIC STUDY OF *ARCTOSTAPHYLOS* AND RELATIVES. VTP = V. Thomas Parker and MV = Michael Vasey. Data in table are listed in the following order: taxa, voucher, herbarium, location (state, county), Genbank accession numbers (ITS1, ITS2).

| | | | |
|--|------------------------------------|--------------------------------|--------------------|
| Subgenus <i>Micrococcus</i> | | | |
| <i>A. mendocinoensis</i> | Wells. McCabe & Shierenbeck 0037. | SFSU. CA, Mendocino. | AF297750, AF297795 |
| <i>A. myrtifolia</i> | Parry. VTP & MV 0497. | SFSU. CA, Amador. | AF297760, AF297805 |
| <i>A. nissenana</i> | Merriam. VTP & MV 0490. | SFSU. CA, El Dorado. | AF297782, AF297727 |
| <i>A. nummularia</i> | A. Gray. Dunne 0040. | SFSU. CA, Marin. | AF297755, AF297800 |
| Subgenus <i>Arctostaphylos</i> | | | |
| Section <i>Arctostaphylos</i> | | | |
| <i>A. bakeri</i> subsp. <i>sublaevis</i> | Wells. VTP & MV 0547. | SFSU. CA, Sonoma. | AF297774, AF297819 |
| <i>A. canescens</i> subsp. <i>canescens</i> | Eastw. MV 0179. | SFSU. CA, Santa Cruz. | AF297781, AF297826 |
| <i>A. catalinae</i> | Wells. VTP & MV 155. | SFSU. Santa Catalina Island. | AF297787, AF297832 |
| <i>A. colombiana</i> | Piper. VTP 0299. | SFSU. CA, Mendocino. | AF297765, AF297810 |
| <i>A. cruzensis</i> | Roof. VTP & Schierenbeck 0012. | SFSU. CA, San Luis Obispo. | AF297750, AF297795 |
| <i>A. glauca</i> | Lindley. VTP 0235. | SFSU. CA, San Luis Obispo. | AF297778, AF29723 |
| <i>A. hispidula</i> | Howell. MV 0360. | SFSU. CA, Del Norte. | AF297752, AF297797 |
| <i>A. hookeri</i> subsp. <i>hookeri</i> | G. Don. Strybing Arboretum. | CA, San Francisco. | AF297756, AF297801 |
| <i>A. mewukka</i> subsp. <i>truei</i> | Knight. MV 0029. | SFSU. CA, Butte. | AF297759, AF297804 |
| <i>A. parryana</i> | Lemmon. J. Keeley 22,291. | LOC. CA, San Bernardino. | AF297757, AF297802 |
| <i>A. patula</i> | Greene. VTP 0313. | SFSU. CA, Sierra. | AF297754, AF297799 |
| <i>A. pechoensis</i> | Abrams. Markos 0264. | SFSU. CA, San Luis Obispo. | AF297767, AF297812 |
| <i>A. peninsularis</i> | Wells. MV 0804. | SFSU. Mexico, Baja California. | AF297785, AF297830 |
| <i>A. stanfordiana</i> subsp. <i>stanfordiana</i> | Parry. MV 0468. | SFSU. CA, Sonoma. | AF297751, AF297796 |
| Subgenus <i>Arctostaphylos</i> | | | |
| Section <i>Foliobracteata</i> | | | |
| <i>A. andersonii</i> | A. Gray. MV 0089. | SFSU. CA, Santa Cruz. | AF297780, AF297825 |
| <i>A. auriculata</i> | Eastw. MV 0170. | SFSU. CA, Contra Costa. | AF297779, AF297824 |
| <i>A. densiflora</i> | Baker. MV 0069. | SFSU. CA, Sonoma. | AF297753, AF297799 |
| <i>A. glandulosa</i> subsp. <i>glandulosa</i> | Eastw. VTP & MV 0157. | SFSU. CA, Santa Barbara. | AF297775, AF297820 |
| <i>A. hooveri</i> | Wells. MV 0667. | SFSU. CA, Monterey. | AF297773, AF297818 |
| <i>A. morroensis</i> | Wiesl. & Schreiber. VTP & MV 0149. | SFSU. CA, San Luis Obispo. | AF297763, AF297808 |
| <i>A. montereyensis</i> | Hoover. VTP 0581. | SFSU. CA, Monterey. | AF297770, AF297815 |
| <i>A. obispoensis</i> | Eastw. VTP & MV 0236. | SFSU. CA, San Luis Obispo. | AF297764, AF297809 |
| <i>A. pajaroensis</i> | Adams. VTP & MV 0459. | SFSU. CA, Monterey. | AF297772, AF297817 |
| <i>A. pallida</i> | Eastw. VTP & MV 0565. | SFSU. CA, Contra Costa. | AF297771, AF297816 |
| <i>A. pilosula</i> | Jepson & Wiesl. VTP 0233. | SFSU. CA, San Luis Obispo. | AF297766, AF297811 |
| <i>A. purissima</i> | Wells. VTP 0238. | SFSU. CA, Santa Barbara. | AF297769, AF297816 |
| <i>A. refugioensis</i> | Gankin. MV 0156. | SFSU. CA, Santa Barbara. | AF297776, AF297821 |
| <i>A. silvicola</i> | Jepson & Wiesl. MV 0082. | SFSU. CA, Santa Cruz. | AF297768, AF297813 |
| <i>A. tomentosa</i> subsp. <i>tomentosa</i> | (Pursh) Lindley. MV 0243. | SFSU. CA, Monterey. | AF297786, AF297831 |
| <i>A. uva-ursi</i> (L.) Sprengel. | MV 0019. | SFSU. CA, San Mateo. | AF297761, AF297806 |
| <i>A. viridissima</i> (Eastw.) McMinn. | MV 0875. | SFSU. CA, Santa Barbara. | AF297777, AF297802 |
| <i>A. viscida</i> subsp. <i>mariposa</i> | (Dudley) Wells. VTP & MV 0569. | SFSU. CA, Tuolumne. | AF297783, AF297828 |
| Subgenus <i>Arctostaphylos</i> | | | |
| Section <i>Pictobracteata</i> | | | |
| <i>A. pringlei</i> subsp. <i>Drupacea</i> (C. Parry) | Wells. MV 0232. | SFSU. AZ, Pima. | AF297784, AF297829 |
| Outgroup | | | |
| <i>Arbutus andrachne</i> | L. UC Botanical Garden. | Israel. | AF297789, AF297834 |
| <i>Arbutus menziesii</i> | Pursh. UC Botanical Garden. | CA, Alameda. | AF086828, AF086828 |

Phylogenetic Analysis of Molecular Data

Molecular data were evaluated using maximum likelihood (ML) and Bayesian methods. ML analyses were performed using PAUP* (Swofford 2003). Bayesian analyses were done using MrBayes version 2.01 (Huelsenbeck and Ronquist 2001). Prior to likelihood or Bayesian analysis of

the best-fit model of evolution was determined using Modeltest (Posada and Crandall, 1998).

Tree searches. Heuristic searches with ten random addition sequence replicates and TBR branch swapping were performed for all ML estimates. Maximum likelihood estimates of the ITS phylogeny were obtained using the TrNef+G model,

which has equal base frequencies and varying transition rates including gamma distribution for rate heterogeneity (Posada and Crandall 1998).

Branch support. Maximum likelihood bootstrap analyses of 100 replicates were performed using a heuristic search with 10 random addition sequence replicates and TBR branch swapping. A Bayesian approach for inferring phylogenies was also used because of its easy interpretation of results, its ability to incorporate prior information (Huelsenbeck and Ronquist 2001), and some computational advantages (Larget and Simon 1999). The analysis used MrBayes (Huelsenbeck and Ronquist 2001), which employs Markov Chain Monte Carlo (MCMC) to approximate the posterior probabilities of phylogenies (Metropolis et al. 1953; Hastings 1970; Green 1995). The model of evolution used for all runs was TrNef+G (determined by ModelTest). MrBayes was run with four chains from 10 different starting points. Five of the 10 runs were 100,000 generations and trees were sampled every 10 generations. The remaining five runs were 1,000,000 generations and trees were sampled every 50 or 100 generations. All 10 runs reached a plateau in likelihood. Trees that were suboptimal at the beginning of the runs were discarded (burn-in phase). All trees saved from all 10 runs were summarized in PAUP* (See MrBayes manual). Posterior probabilities for nodes of interests were recorded in Table 2.

Morphological constraint trees. To test the monophyly of species with shreddy bark, unequal stomata, scale-like bracts and chromosome number all species in our data set with a particular character were constrained to a monophyletic group. These characters were chosen because they have been used for distinguishing species or higher taxa in previous treatments (Adams 1940; McMinn 1939; Wells 1969, 1992). All character states were extracted and defined by Wells (1992) and confirmed by the authors both on herbarium sheets and in the field. Each species set was tested using both the Kishino-Hasegawa (1989) and the Shimodaira-Hasegawa (1999) tests in a likelihood context to compare competing tree topologies. For tests, settings were set to full-optimization with 1000 bootstrap replicates. All analyses were performed using PAUP*.

RESULTS

Missing data represented zero percent of the data set. There were 120 phylogenetically informative sites out of 531 base pairs for ITS 1 & 2 including all taxa listed in Table 1. Uncorrected P values among species range from 0.0 to 0.09. Base frequencies were: A = 0.24147, C = 0.24423, G = 0.24133, T = 0.27297. Base composition bias was calculated as 0.03, showing minimal bias. A g_i statistic of -1.356 (SD = 13.18) was calculated indicating significant structure in the data set.

TABLE 2. PARAMETERS USED IN MRBAYES RUNS. Nodes A, B, C and D are labeled on Fig. 1. Probabilities are expressed as posterior probabilities of all trees (omitting burn-in trees).

| Run | Number of generations | Tree sample frequency | Suboptimal trees (burn-in) | Number of trees | Likelihood (final tree) | Probability clade A | Probability clade B | Probability clade C | Probability clade D |
|-----|-----------------------|-----------------------|----------------------------|-----------------|-------------------------|---------------------|---------------------|---------------------|---------------------|
| 1 | 100,000 | 10 | 1-3,187 | 6,813 | -2618.26 | 65 | 64 | 73 | 51 |
| 2 | 100,000 | 10 | 1-2,325 | 7,675 | -2615.09 | 68 | 56 | 60 | 59 |
| 3 | 100,000 | 10 | 1-1,885 | 8,115 | -2622.73 | 71 | 69 | 76 | 58 |
| 4 | 100,000 | 10 | 1-2,597 | 7,403 | -2613.45 | 69 | 78 | 87 | 59 |
| 5 | 1,000,000 | 100 | 1-306 | 9,694 | -2630.15 | 51 | 65 | 67 | 79 |
| 6 | 1,000,000 | 100 | 1-288 | 9,712 | -2621.01 | 56 | 69 | 71 | 64 |
| 7 | 1,000,000 | 100 | 1-268 | 9,732 | -2625.63 | 55 | 75 | 76 | 71 |
| 8 | 1,000,000 | 100 | 1-218 | 9,782 | -2628.85 | 59 | 67 | 68 | 62 |
| 9 | 1,000,000 | 50 | 1-255 | 19,745 | -2627.74 | 59 | 67 | 68 | 62 |
| 10 | 1,000,000 | 50 | 1-646 | 19,354 | -2618.80 | 53 | 64 | 64 | 60 |

Phylogenetic Analyses

A ML search resulted in one most likely tree (Fig. 1, $-\ln = 2025.40$). There is relatively strong support along the backbone of the *Arctostaphylos* phylogeny (Fig. 1) and weaker branch support on the tips. There is a deep split (nodes labeled A and B in Fig. 1) in the phylogeny for *Arctostaphylos* (Fig. 1). We have labeled the two clades that result in the splits at both “A” and “B” Clade 1 and Clade 2 respectively. The deep split into two lineages is marginally supported by both a ML bootstrap (60 and 70) and posterior probabilities from Bayesian analyses (Table 2). There are two other nodes that are well supported along the backbone of the phylogeny, nodes C and D. Other relationships supported by both ML bootstrap and Bayesian runs are: *A. pechoensis* and *A. purissima* (100/98, posterior probability/ML bootstrap), *A. viridis-sima* and *A. cruzensis* (89/86), *A. nissenana* and *A. viscida* (100/98), and *A. pringlei* and *A. peninsularis* (100/99).

All 10 runs of MrBayes differed slightly in number of trees included in final summary tree, number of burn-in trees, and posterior probabilities (Table 2). Nodes A, B, C, and D (Fig. 1) are of interest because they are the nodes that define clades along the backbone of the phylogeny. There are six other clades in the phylogeny supported by posterior probability and not a ML bootstrap value (Fig. 1).

Morphology Constraint Trees

All constrained ML searches of morphological characters (i.e., shreddy bark, unequal stomata, type of bracts and chromosome number) resulted in significantly less likely trees (Table 3). Constraining the species with shreddy bark resulted in the biggest difference in likelihood (54.796) while chromosome number resulted in the smallest difference (27.277).

DISCUSSION

Phylogenetic Analyses and Relationships

The two clades in the *Arctostaphylos* ITS phylogeny (Fig. 1) present a different model of evolution than have relationships based on morphology (e.g., Wells 1992, 2000). One clade consists of *A. mendocinoensis*, *A. stanfordiana*, *A. hispidula*, *A. densiflora*, *A. hookeri* subsp. *hookeri*, *A. nummularia*, *A. parryana*, *A. patula*, *A. mevuikka* and *A. myrtifolia*. The second clade contains the remaining 28 taxa sampled in this study. The results found here agree with those of Markos et al. (1998) who also found two groups within a 26S sequence tree of *Arctostaphylos*.

The ML phylogeny and the Bayesian analyses for the ITS data do not support Wells’ (1992, 2000) classification. In these analyses, subgenus *Micrococcus* is not monophyletic, and two sections of subgenus *Arctostaphylos* proposed by Wells (1992,

2000), section *Foliobracteata* and section *Arctostaphylos*, are clearly not monophyletic (Fig. 1, Tables 2 and 3). The strongly supported clades along the backbone of the ITS phylogeny show this. The incongruence between the morphologically based classification and Fig. 1 suggests a different interpretation of the evolution of the genus. For example, common to both trees are species with elliptic, simple green leaves like *A. pungens* and *A. pringlei* in one clade, *A. hookeri* ssp. *hookeri* and *A. densiflora* in the other, similar in shape to ancestral fossil leaves of *Arctostaphylos* from the Miocene and Pliocene (Chaney and Mason 1934; Mason 1934; Axelrod 1950; Wolfe 1964). Other processes that would influence a morphological approach are hybridization, allopolyploidy or convergence.

Hybridization has been postulated as an important factor in the evolution of *Arctostaphylos* (Stebbins and Major 1965; Shapin 1966; Gottlieb 1968; Raven and Axelrod 1978; Roof 1978; Kruckberg 1977; Schierenbeck et al. 1992). Further directions might include looking at known hybrids and their parental origin in a molecular phylogenetic framework. McDade (1992, 1997) has employed parsimony techniques to show how hybrids affect phylogenies; this technique, along with maximum likelihood and a Bayesian analysis might shed light on hybridization of *Arctostaphylos* taxa and how they affect phylogenies. Hardig et al. (2000, 2002) have used sequence data to examine species of putative hybrid origin in *Ceanothus* although they could not rule out allopatric origins.

Constraint Trees

The morphological characters that were included in this study were type of bracts, type of bark, stomatal distribution, and ploidy level. Of these characters, only bract type has been suggested to be monophyletic, while the others have been used to segregate smaller sets of species or subspecies. The sections of subgenus *Arctostaphylos* described by Wells (1992), for example, are defined based in part on bract type. Nineteen species of the leafy bracted group (section *Foliobracteata*) and sixteen species with a scale-like bract (section *Arctostaphylos*) were included in our study. These two sections of subgenus *Arctostaphylos* do not form monophyletic groups in Fig. 1 and when the constraint of bract type was carried out (Table 3) the resulting tree was significantly different than the unconstrained phylogeny. Based on our study, bract shape in *Arctostaphylos* is not a phylogenetically useful character at the sectional level in the genus.

In Wells’ (1992) classification, bark characteristics generally are given minor significance in the taxonomy of the group. Species with rough or shreddy bark fall into both subgenera and sections. Although not recognized by Wells (1992), northern populations (Mendocino Co.) of *A. nummularia* have shreddy bark in contrast to southern popula-

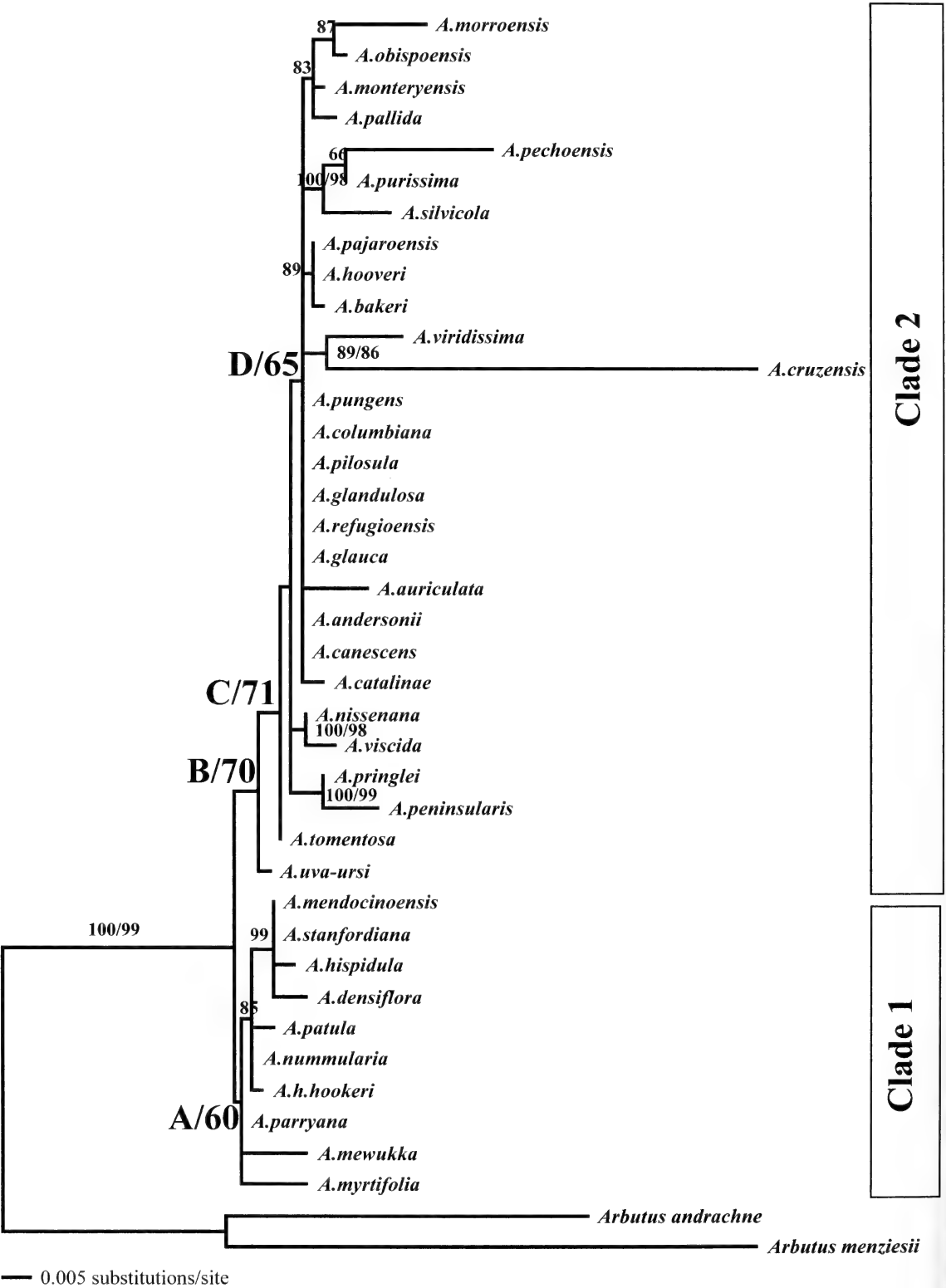


FIG. 1. Maximum likelihood tree generated using ITS data and the TrNef+G model of evolution ($-\ln = 2025.4027$). A Bayesian analysis was run under the TrNef+G model (see Table 2 for parameters) to assess the posterior probabilities of the nodes. Numbers above the nodes are posterior probabilities/maximum likelihood bootstrap when two numbers are present and posterior probabilities when one number is shown. Letters above the nodes correspond to letters in Table 2.

TABLE 3. TOPOLOGY TEST STATISTICS. KH = Kishino-Hasegawa, SH = Shimodaira-Hasegawa. (Kishino and Hasegawa 1989; Shimodaira and Hasegawa 1999). Morphological character data were obtained from Wells (1992) and confirmed by the authors.

| | LN | Difference | KH-test P-value | SH-test P-value | Significant |
|-------------------|-------------|------------|--------------------|--------------------|-------------|
| Shreddy bark | | | | | |
| Tree1 | -2025.40271 | best | | | |
| Tree2 | -2080.19954 | 54.79682 | 0.000 | 0.006 | YES |
| Stomata unequal | | | | | |
| Tree1 | -2025.40271 | best | | | |
| Tree2 | -2070.89644 | 45.49373 | 0.000 | 0.008 | YES |
| Scale-like bracts | | | | | |
| Tree1 | -2025.40271 | best | | | |
| Tree2 | -2060.60708 | 35.20437 | 0.000 | 0.015 | YES |
| Chromosome Number | | | | | |
| Tree1 | -2025.40271 | best | | | |
| Tree2 | -2052.68067 | 27.27796 | 0.000 | 0.018 | YES |

tions of Marin, San Mateo and Santa Cruz Counties; in the same Wells' subgenus, *A. nissenana* also exhibits roughened grey bark. In subgenus *Arctostaphylos* (Wells 1992), *A. tomentosa*, *A. morroensis*, *A. rudis*, *A. pajaroensis* and several others have shreddy, gray bark. We found that a monophyletic group constrained on the ITS tree was significantly different from the unconstrained tree suggesting this character has arisen more than once. Hileman et al. (2001) found a similar result in *Arbutus* in which multiple species have either smooth reddish or roughened grayish bark but neither represents a monophyletic group.

Some members of *Arctostaphylos* have stomata on both sides of the leaf (isofacial), others have stomata on the underside of the leaf (bifacial), and some have more stomata on the bottom than on the top (heterofacial). Wells (1992) reports that there are 10 species of *Arctostaphylos* with bifacial/heterofacial leaves: *A. tomentosa*, *A. andersonii*, *A. pajaroensis*, *A. morroensis*, *A. uva-ursi*, *A. pumila*, *A. edmundsii*, *A. insularis*, *A. nummularia* and *A. mendocinoensis*. Ecologically, the bifacial/heterofacial species are restricted to the cooler, mild climate of the coastal fog belt (Wells 1992). We have included seven of the 10-bifacial/heterofacial species in our study: *A. mendocinoensis*, *A. nummularia*, *A. uva-ursi*, *A. pajaroensis*, *A. andersonii*, *A. tomentosa* and *A. morroensis*. When bifacial/heterofacial species are constrained to form a monophyletic group, the ML estimate is significantly different from the non-constraint tree (Table 3). Therefore, stomatal distribution likely has arisen independently in some of these species and is likely to have resulted from ecological convergence.

The majority of *Arctostaphylos* have a base chromosome number of *n* = 13 while others have *n* = 26 (Wells 1992). There are only two tetraploids in clade one (*A. parryana* and *A. mewukka*) and three in clade two (*A. bakeri*, *A. glandulosa* and *A. to-*

mentosa). When constraining all tetraploids to a monophyletic group a significant increase in likelihood resulted (Table 3) indicating the support that is present along the backbone of the phylogeny is significant. Figure 1 is also useful in looking at the hypothesis of Roof (1980). Roof (1980) hypothesizes that through the boreal species *A. uva-ursi*, a great gene pool of *Arctostaphylos* at the tetraploid level has entered California from the north while another vast gene pool, at the diploid level has come to California in *A. pungens*, a species derived from Mexico and the American southwest. We do not find support for Roofs' hypothesis based on the placement of *A. pungens*, which is embedded in "Clade two". If Roofs' hypotheses were supported we would expect to see *A. pungens* at the base of the two clades.

The results presented here suggest that a thorough reexamination of the current classification of *Arctostaphylos* is warranted. If hybridization and polyploidy are both important processes for evolution in this genus, then morphological characters may not consistently represent monophyletic groups. Introgression and hybridization can also influence the interpretation of molecular-based phylogenies. Because species within *Arctostaphylos* are known to hybridize (e.g., Gottlieb 1968) and some neutral characters spread across species boundaries (e.g., Ellstrand et al. 1987), molecular trees based on neutral molecular characters like the ITS region of the nuclear ribosome may be subject to similar problems. Hardig et al. (2000), for example, developed an ITS tree for *Ceanothus* that illustrated a few anomalies, such as a few examples of taxa with geographic proximity being clustered together, while taxa with morphologically unique characters (such as the two varieties of *C. jepsonii* with six-merous flowers) were separated. In another study, Schierenbeck et al. (1992) provided evidence for the hypothesized allopolyploid origin of *A. mewukka*.

ka from a hybrid cross between *A. viscida* and *A. patula*. In this study, these two latter species are in different clades; but this allopolyploid indicates a potential problem for interpretation of both morphological and molecular features. (*A. Mewukka* is found only near one of the parents.) Markos et al. (1998) found *A. pungens* to be ambiguous in its placement based on RFLPs while it fell clearly into the larger clade in this study. All of these results suggest caution with both morphological and molecular approaches in *Arctostaphylos*. This ITS phylogeny should be taken as an alternative to previous morphological models of the genus.

While this molecular tree is not the only way to assess relationships in this group, research on hybridization in *Arctostaphylos* differentially supports it over previous models of evolution in this genus based on morphology. Dobzhansky (1953) concluded his study of hybridization in *Arctostaphylos* with the comment that there was little indication of the loss of species boundaries and just a small number of hybrids. He examined two diploid species (*A. viscida* and *A. patula*) in his study to assess whether there was some type of reproductive isolating mechanism. The co-occurrence of these and other pairs of diploid species that do not show extensive hybridization (e.g., *A. nummularia* and *A. silvicola* in the southern Santa Cruz Mts, *A. pechoensis* and *A. hookeri* near Prunedale, CA) all have one feature in common: these pairs of diploid species each combine a representative from both clades. This suggests the ITS molecular tree more accurately distributes species by their reproductive closeness, as studies in which hybridization was low (e.g., Dobzhansky 1953) combine species from both clades, while studies in which hybridization was abundant (e.g., Gottlieb 1968, Schmid et al. 1968) examined species pairs from one of the clades indicated in the ITS tree.

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A GENETIC AND MORPHOLOGICAL STUDY OF *CLARKIA STELLATA*
(ONAGRACEAE) AND RELATED SPECIES IN
NORTHEASTERN CALIFORNIA

KRISTINA A. SCHIERENBECK¹, LAWRENCE JANEWAY, ANIL KAPOOR, AND
FRANCIS PHIPPS

California State University Chico, Department of Biology, Chico, CA 95929-0515

ABSTRACT

Clarkia stellata Mosquin (Onagraceae) is an uncommon annual herb endemic to Plumas and Yuba Counties in northeastern California that has threatened populations due to noxious weeds, recreational and forest management activities, and development. The purpose of this study is clarify the species identification of populations of *Clarkia stellata* for management purposes, specifically, populations of *C. stellata* and *C. rhomboidea* that are difficult to differentiate in the field. A total of 11 populations of *C. stellata* and related species were sampled for morphometric analyses and nine populations were sampled for genetic analysis using amplified fragment length polymorphisms (AFLPs). *Clarkia stellata* can be separated from *C. rhomboidea* based on all floral characteristics except claw width, claw length, and isthmus width. These species also can be differentiated based on the following vegetative characteristics: petiole length, leaf length, leaf width, and plant height. The sympatric *Clarkia mildrediae* is easily differentiated from *C. stellata* by every character except petiole length, leaf length, and plant height; *C. mildrediae* differs from *C. rhomboidea* for all characters except petal speckling, pollen color, leaf width, and leaf length. Populations that were initially difficult to categorize as either *C. stellata* or *C. rhomboidea* were most similar to *C. stellata*; however, we were not able to identify a suite of characters that would distinguish these populations as either *C. stellata* or *C. rhomboidea*. An analysis of molecular variance (AMOVA) shows that although there was genetic variation among all populations (13.19%), the majority of variation is found within populations (86.81%). Genetic differentiation among all populations was low as calculated by Genetic Data Analysis ($\Phi_{st} = 0.132$) and Hickory ($\theta^B = 0.0137$); variance within populations was high (sigma-G = 32.645) and between populations was low (sigma-P = 4.96).

This work is consistent with a number of studies within *Clarkia* section *Myxocarpa* that have identified taxonomic difficulties due to recent speciation, local adaptation, rapid chromosomal evolution, sympatry, and hybridization.

Key Words: *Clarkia*, Amplified Fragment Length Polymorphisms, rare species, morphometrics, rapid evolution.

Clarkia stellata Mosquin (Onagraceae) was described from Lake Almanor, Plumas County and nearby Yuba County in Northeastern California (Mosquin 1962); it is now known to occur uncommonly in coniferous forest openings at elevations from 1000 to 1500 m within Plumas, Tehama, Nevada, Placer, and Yuba counties (Lewis 1993).

Threats to populations of *C. stellata* include noxious weeds, timber harvest activities, reforestation, livestock grazing, lack of fire, fire fighting/suppression activities, spring prescribed burning, camping, mining, road construction and maintenance, and development (Van Zuuk 2000). *Clarkia stellata* is not listed as rare, endangered, or threatened by the state or federal government; however, because of its uncommon occurrence, it is considered a "sensitive species" by the U.S. Forest Service (Van Zuuk 2000).

Clarkia stellata is included within *Clarkia* section *Myxocarpa* which includes the diploid species *C. australis* Small, *C. borealis* Small, *C. mildrediae*

(Heller) Lewis and Lewis, *C. mosquinii* Small, *C. virgata* Greene, and the polyploid *C. rhomboidea* Douglas (Small 1971a). *Clarkia stellata* and *C. rhomboidea* are presumed to be autogamous based on simultaneous maturation of the stigma and anther. Extensive hybridization and chromosomal analyses strongly support that *C. stellata* originated as a result of one or more reciprocal translocations in *C. mildrediae* (Mosquin 1961; Small 1971a, b).

Although *Clarkia stellata* is morphologically most similar to *C. rhomboidea*, based on chromosomal evidence, *C. rhomboidea* is hypothesized to have formed from hybridization between *C. virgata* and *C. mildrediae* (Mosquin 1964). *Clarkia rhomboidea* is common in yellow pine forests and woodlands at elevations less than 2500 m throughout the California Floristic Province and beyond. Although Small (1971) noted that *C. stellata* tends to occur on more xeric microsites than *C. rhomboidea*, these species often occur sympatrically and are indistinguishable in the vegetative state. Sympatric is defined here as occurring in close proximity but not in mixed populations, with the exception of the "*C. stellata/rhomboidea*" populations, which are mixed.

¹ Author for correspondence, email: kschierenbeck@csuchico.edu

TABLE 1. MORPHOLOGICAL CHARACTERS FOR CLARKIA STELLATA, C. RHOMBOIDEA, C. MILDREDIAE, AND C. MOSQUINII AS PROVIDED BY LEWIS (1993). Abbreviations: lbd = lobed; incons. = inconspicuously.

| Species | Petal length (mm) | Petal spotting | Claw/Blade | Stigma > anthers? | Chromosome # | Pollen color |
|---------------|----------------------|----------------------|------------------------------|-------------------------|-----------------|---------------------|
| C. stellata | 6–8 | no | claw 2-lbd/ incons. 3-lbd | no | n = 7 | yellow |
| C. rhomboidea | 7–14 | generally spotted | claws 2-lbd/ unlobed | no | n = 12 | blue-gray |
| C. mildrediae | 15–20 | flecked/ spotted | claw 2-lbd/ unlobed | yes | n = 7 | light blue/ blue |
| C. mosquinii | 15–20 | purple spotted | claw 2-lbd/ unlobed | yes | n = 6 | blue-gray |

Species within *Clarkia* section *Myxocarpa* are notoriously difficult to distinguish in the field (Small 1971; Gottlieb and Janeway 1995). Although some morphological characters superficially separate the Section *Myxocarpa* species that occur sympatrically in northeastern California (*C. stellata*, *C. rhomboidea*, *C. mildrediae*, and *C. mosquinii* [Table 1; Lewis 1993]) overlapping variation has been identified frequently in the field (L. Janeway personal observation).

The purpose of this study is not to provide a definitive study of members of *Clarkia* section *Myxocarpa* but is to clarify the identification of populations of *C. stellata* for management purposes. Specifically, populations of *C. stellata* and *C. rhomboidea* in northeastern California are often difficult to differentiate, and our null hypothesis is that populations of these species cannot be separated morphologically and genetically.

MATERIALS AND METHODS

Morphometric Data Collection

Two populations ambiguously identified as *Clarkia* “*stellata/rhomboidea*”, known populations of *C. stellata* (six) and *C. rhomboidea* (two), and one population of *C. mildrediae* (included because of its sympatry with a *C. stellata/rhomboidea*” population) were sampled in June and July 2001 (Table 2). In the “*C. stellata/rhomboidea*” populations, individuals were selected for analyses based on their ambiguous morphological characters. *Clarkia mosquinii* was not included in this study because of its rarity, it is not easily confused with the other study species, and it has not been reported growing with *C. stellata*. Populations were sampled based on records provided by the U.S. Forest Service and based on an *a priori* determination that used the characters provided by Lewis (1993). Some difficulty was encountered in finding populations with enough flowering plants for adequate sampling due to low rainfall during the winter of 2000–2001. Material was collected from a total of 210 individuals, where n = 16–20 per population. Voucher specimens for all populations are on file at the CSU Chico Herbarium (CHSC).

We followed the protocol of Gottlieb and Ford (1999) for petal measurements and collected only from plants that had open stigmas. The following floral characteristics were measured: limb width, “isthmus” width at the narrowest point, claw width, and claw length. Petal speckling was assigned a value of 1 (none), 2 (slight), 3 (sparse), 4 (moderate), and 5 (dense). Pollen color was assessed on fresh material in the field and assigned a value of 1 (yellow and light yellow), 3 (light green), and 5 (light blue and blue). The vegetative characters, leaf length, leaf width, petiole length, and plant height were also measured.

Morphometric Data Analysis

Descriptive statistics were calculated for each population for all measured characteristics. Differences among “species” categories were analyzed using a Kruskal-Wallis One Way Analysis of Variance on Ranks. All pairwise multiple comparison procedures were calculated using Dunn’s method. Petal speckling is often cited as a key character, thus we performed a multiple linear regression analysis between this and all other morphological characteristics to estimate its reliability in identifying the study species. All morphological statistics were calculated using SigmaStat 3.2 (SPSS, Inc. CA USA).

Genetic Data Collection

Leaf samples were put on ice and directly transported to California State University, Chico (CSU Chico), where they were stored at –80°C until DNA extraction. Genomic DNA was extracted from the same individuals used in the morphometric analysis using a Fast Prep Kit (Bio 101, Inc); however, population sample sizes ranged from 6–20, and the HUMB and MDWV populations were not included, due to difficulties in the extraction and PCR process. DNA concentrations were determined using a GeneQuant (Pharmacia Biotech), and the samples stored at –20°C until needed.

AFLP digestion, ligation, and PCR-amplifications were carried out using an AFLP Analysis System (Vos et al. 1995; GibcoBRL, Life Technolo-

TABLE 2. COLLECTION LOCATIONS FOR *CLARKIA STELLATA*, *C. RHOMBOIDEA*, *C. "STELLATA/RHOMBOIDEA"*, AND *C. MILDREATAE* POPULATIONS. PSME = *Pseudotsuga menziesii*, MCF = Mixed conifer forest, YPF = Yellow pine forest, ABCO = *Abies concolor*, PIJE = *Pinus jeffreyi*, PIPO = *Pinus ponderosa*, LIDE2 = *Lithocarpus densiflora*.

| Population/ Coll. date | Forest type | Elev. | Lat./Long. | U.S.G.S. Topo. Map |
|--|--------------------|---------|--------------------------|--|
| <i>Clarkia stellata</i> | | | | |
| CALF 6-15-01 | PSME-MCF | 1402 m | 40°09'39", 121°31'43" | Onion Butte, se ¼ of sw ¼ sect. 23, T27N, R4E |
| Comments: Population numbers in 1000's (<i>Janeway 7174</i> CHSC). Mid to late flowering, ca. 25% w/fruits only. Slope 40°, aspect SW. Above N. Fork of Calf Creek, 1.6 km N-NW of Colby Mtn. and between 27N12 and 27N06. A clearcut unit, shrubs dominate, especially <i>Ceanothus intergerrimus</i> , 3.5 m tall. Pines planted 5–6 years old, 1 m fall. Burned following harvest. Stigma receptive, stigmas shorter than stamens, pollen "light green" | | | | |
| HUMB 6-15-01 | YPF-ABCO | 1384 m | 40°12'38", 121°12'27" | Almanor, nw & sw ¼ of sw ¼ sect. 9, T27N, R7E |
| Comments: Population approx. 400 plants (<i>Janeway 7179</i> CHSC). Slope ~0°, aspect southerly. E. side of Humbug Rd ca. 2.72 km SW of shore of Lake Almanor, 4 km W of Prattville. Rocky volcanic, <i>Clarkia stellata</i> esp. where rock outcrops to surface and fractures (less logging and disturbance). Stigma receptive w/pollen. Anthers dehiscent, anther sacs and pollen yellow. | | | | |
| MDWV 6-14-01 | PSME-MCF | 1329 m | 39°54'54", 121°00'20" | Meadow Vly, sw ¼ of nw ¼ sect. 29, T27N, R9E |
| Comments: Population approx. 500 plants (<i>Janeway 7173</i> CHSC). Approx. 75% in fruit only. Slope 10–35°, aspect S, SW. Deep soil, lightly rocky, sandstone/shale substrate. "Plantation" recently thinned, probably brushed, partly burned including tractor trails. Stigmas receptive w/pollen. | | | | |
| CONE 6-28-01 | YP-MCF | ~1768 m | 40°41'36", 121°07'11" | Harvey Mountain, sect. 30 T33N, R8E |
| Comments: Population approx. 200 plants (<i>Janeway 7233</i> CHSC). Approx. 5% in bud, 45% in flower, and 50% in fruit. Slope 10°, aspect SW. SW flank of Cone Mtn, 0.48 km SW of the summit and along road. Fairly consistent speckling, pollen color, and anther sac color. | | | | |
| MONT 6-24-01 | PIJE-MCF | 1676 m | 40°16'54", 121°39'28" | Lyonsville se ¼, of nw ¼ sect. 17, T28N, R3E |
| Comments: Population approx. 500 plants (<i>Janeway 7216</i> CHSC). Approx. 10% in bud, 60% in flower, and 30% in fruit. Slope 10–20°, aspect SW. On Monterey Point ridge 0.16 km SW of Rd 29N48; ca 4 km SW of Turner Mtn. SW-trending ridgetop. The red-orange anthers are often quite showy, esp. when not open all the way. Stigma receptive and coated with pollen. | | | | |
| WILL 6-19-01 | YPF-MCF | 1658 m | 40°24'20", 121°21'36" | Mt. Harkness nw ¼ of nw ¼ sect. 6, T29N, R6E |
| Comments: Population approx. 400 plants (<i>Janeway 7185</i> CHSC). Approx. 30% in bud, 60% in flower, and 10% in fruit. Slope 30–40° aspect S, SW. Willow Lake at scattered locations along the north side of the lake, above trail 3–15 m. Rocky volcanic. Areas with <i>Clarkia stellata</i> fairly to quite exposed in afternoon. | | | | |
| <i>Clarkia rhomboidea</i> | | | | |
| JCTH 6-17-01 | PSME-MCF- LIDE2 | 1008 m | 39°43'40", 121°18'06" | Brush Crk. sw ¼ of sw ¼ sect. 27, T22N, R6E |
| Comments: Population > 300 plants (<i>Janeway & Castro 7183</i> CHSC). Approx. 10–20% in current and recent flower and rest in fruit. Slope 40–50°, aspect SW. 1.6 km SW of Junction House along Rd22N49 parallel to and about 100 m of OroQuincy Hwy. revegetating PIPO plantation. Pollen blue, anther sacs magenta like filaments and style, stigmas receptive, longer than usual, just > anthers, bend down away from anthers. **Chromosome counts (Gottlieb & Janeway 1995) verify this population as <i>C. rhomboidea</i> . | | | | |
| GANS 6-28-01 | PSME-MCF | 1069 m | 40°02'12", 121°13'39" | Caribou, nw ¼ of sw ¼ sect. 8, T25N, R7E |
| Comments: Population approx. 200 plants (<i>Janeway 7238</i> CHSC). Approx. 10% in bud, 30% in flower, and 50% in fruit. Slope 50°, aspect S, SE. On slope of ridge overlooking North Fork Feather River, and Caribou Road ca. 2.56 km N of confluence of E. Br. N. Fk. Feather River and along rd 3.36 km from Caribou Road. | | | | |

gies, 1996) with some modifications. Approximately 250 nm of genomic DNA were double digested with the restriction enzymes *Eco*R1 and *Mse*I. The DNA and enzymes were mixed with a reaction buffer (50mM Tris-HCl (pH 7.5), 50 mM Mg-acetate, 250 mM K-acetate), and distilled water,

placed in a thermocycler for 2 hr at 37°C and incubated period at 70°C for 15 min. The samples were then cooled, adapters and DNA ligase added, and the mixture incubated for 2 hr at 20°C.

The DNA was diluted with TE buffer to a concentration of 1:10 and used in the first of two PCR

TABLE 2. CONTINUED.

| Population/ Coll. date | Forest type | Elev. | Lat./Long. | U.S.G.S. Topo. Map |
|---|-------------|----------------|--------------------------|---|
| <i>Clarkia rhomboidea/Clarkia stellata</i> | | | | |
| WATS 7-3-01 | PIPO-MCF | 1707 m | 38°50'22° 121°02'45" | Dogwood Pk, ne ¼ of se ¼ sect. 23, T23N, R8E |
| Comments: Population approx. 200 plants (<i>Janeway</i> 7258 CHSC). Approx. 10% in bud, 50% in flower, and 40% in fruit. Slope 20–35°, aspect S. Top of S-facing slope overlooking mid fork Feather River and head of Sherman Creek. A couple of <i>Clarkia mildrediae</i> ssp. <i>lutescens</i> in bud but the <i>Clarkia mildrediae</i> population is about 100 m east, flowering and without <i>C. stellata/C. rhomboidea</i> . | | | | |
| HRIM 6-21-01 | YPF-MCF | 1524–1585 m | 40°41'55", 121°23'35" | Old Station, sect. 23 and 26 T33N, R5E |
| Comments: Population approx. 800 plants (<i>Janeway</i> 7215 CHSC). Approx. 0% in bud, 10% in flower, 90%. Slope 20–35°, aspect NE. On top of Hat Creek Rim, 3.52 km NE of Old Station. Only about 25% as many plants as last year. | | | | |
| <i>Clarkia mildrediae</i> | | | | |
| WATM 7-3-01 | PIJE-MCN | 1707 m | 39°50'23", 121°02'40" | Dogwood Pk, nw ¼ of sw ¼ sect. 24, T23N, R8E |
| Comments: Population approx. 500 plants (<i>Janeway</i> 7267 CHSC). Approx. 20% in bud, 80% in flower, and 0% in fruit. Slope 40°, aspect S–SW. Top of S–SW facing slope overlooking mid fork Feather River and head of Sherman Creek. Soil volcanic, somewhat rocky. | | | | |

programs. The samples were prepared for the first program by the addition of pre-amplification primer mix (0.94 µg/mL *Eco*R1 adapter, 0.94 µg/mL *Mse*I adapter, 10mM dNTP's), 10X PCR buffer plus MgCl₂, and *Taq* polymerase. The PCR program was as follows: 94°C for 30 sec, 56°C for 60 sec, and 72°C for 60 sec for 20 cycles. The PCR product was diluted to a concentration of 100 ng of DNA.

The final PCR reaction was run with diluted DNA PCR product and two mixes. In mix 1, the *Eco*R1 and *Mse*I primers were selected and mixed together. Ten primer combinations were screened and ultimately, two AFLP primer set combinations (*Eco*R1/*Mse*I) were used to identify polymorphisms within and among populations. In mix two, 10X PCR buffer, distilled water, and *Taq* polymerase were mixed. Mix 1 and 2 were then combined with the diluted DNA and underwent the following PCR conditions: 94°C for 1 min, 65°C for 1 min; and 72°C for 1 min, 30 sec for 23 cycles.

AFLP-PCR products were separated electrophoretically on a non-denaturing 6% polyacrylamide gel at 1000 volts for two hours. The resulting banding patterns were visualized using silver staining (Cho et al. 1996). The gels were dried overnight and photographed using APC (automatic processor compatible) film from Promega (catalog # Q441) and a light table. The light exposed photo paper was developed using an X-ray film-processing machine.

Genetic Data Analysis

Presence (1) or absence (0) data from the AFLP gels were collected for each individual via manual scoring. Only fragments that were unambiguous were included in the analysis. These data were used

to calculate genetic similarities using Pairwise squared Euclidean distances (Excoffier et al. 1992) constructed with a Euclidean Matrix Macros in Microsoft Excel (2000). Genetic similarities among populations were analyzed by the AMOVA program (version 1.55; Excoffier et al. 1992), which allows calculation of variance components and significance levels on several hierarchical levels, including within and among populations (Schierenbeck et al. 1996; Schmidt and Jensen 2000). PAUP version 4.0b8 was used to generate a Neighbor-Joining phylogram with the Upholt option in order to show associations among populations (Swofford 1998). Within population statistics for expected heterozygosity (He) and polymorphic loci (P) were calculated using Genetic Data Analysis (Lewis and Zaykin 2002). Hickory version 1.0 (Holsinger et al. 2002; Holsinger and Lewis 2003) was used to calculate the population statistics, *f* and θ^B, analogous to the *F*-statistics (Wright 1969) *F*_{IS} and *F*_{ST}, respectively. We used the Hickory default values for burn-in (50,000), sampling (250,000), and thin (50). Hickory uses Bayesian methods and specifically here, the Deviance Information Criterion (DIC), which fits the *f* model to the data, and allows a determination of inbreeding within populations or genetic differentiation among populations.

RESULTS

Morphological Analysis

Descriptive statistics for morphological characteristics are provided for all populations (Table 3). An ANOVA by species categorization indicates there are significant differences between *C. stellata* and *C. rhomboidea* for all characters except claw

TABLE 3. MORPHOMETRIC ANALYSIS FOR *CLARKIA STELLATA*, *C. RHOMBOIDEA*, *C. "STELLATA/RHOMBOIDEA"*, AND *C. MILDREATAE* POPULATIONS IN NORTHERN CALIFORNIA. See Table 2 for population and species abbreviations. All values are means and standard errors, and values are in mm with the exception of plant height (dm) and pollen color and petal speckling (see materials and methods).

| Species | Population | Petal claw length | Total petal length | Petal claw width | Petal isthmus width | Petal limb width |
|---------|------------|-------------------|--------------------|------------------|---------------------|------------------|
| CLST | CALF | 1.65 (0.030) | 7.66 (0.102) | 2.12 (0.045) | 1.53 (0.031) | 4.22 (0.095) |
| CLST | MDWV | 1.36 (0.044) | 6.39 (0.188) | 2.15 (0.062) | 1.75 (0.266) | 3.85 (0.113) |
| CLST | WILL | 1.49 (0.028) | 7.36 (0.120) | 1.96 (0.032) | 1.68 (0.028) | 4.08 (0.109) |
| CLST | CONE | 1.74 (0.107) | 7.62 (0.235) | 1.56 (0.068) | 1.49 (0.048) | 4.19 (0.167) |
| CLST | HUMB | 1.25 (0.059) | 6.58 (0.153) | 1.74 (0.059) | 1.62 (0.053) | 3.91 (0.117) |
| CLST | MONT | 1.58 (0.050) | 7.29 (0.122) | 2.16 (0.047) | 1.68 (0.023) | 4.68 (0.116) |
| CLRH | JCTH | 2.63 (0.086) | 10.37 (0.290) | 2.28 (0.068) | 1.90 (0.036) | 5.65 (0.231) |
| CLRH | GANS | 1.79 (0.067) | 9.11 (0.236) | 1.91 (0.034) | 1.62 (0.034) | 5.01 (0.164) |
| ST/RH | WATS | 1.63 (0.037) | 7.68 (0.150) | 2.49 (0.061) | 1.91 (0.040) | 4.77 (0.122) |
| ST/RH | HRIM | 1.76 (0.097) | 8.10 (0.252) | 1.90 (0.065) | 1.78 (0.061) | 5.03 (0.218) |
| CLMI | WATM | 4.05 (0.107) | 17.71 (0.248) | 4.04 (0.103) | 2.91 (0.102) | 12.49 (0.212) |

| | Petiole length | Leaf length | Leaf width | Pollen color | Petal speckling | Plant height |
|-------|----------------|---------------|---------------|---------------|-----------------|--------------|
| CLST | 14.95 (0.928) | 48.05 (2.107) | 11.80 (0.675) | 3 (0) | 2 (0) | 4.65 (0.189) |
| CLST | 13.80 (0.907) | 44.70 (2.608) | 13.80 (0.694) | 1 (0) | 1.85 (0.082) | 4.18 (0.347) |
| CLST | 10.80 (0.462) | 47.50 (1.946) | 13.20 (0.866) | 3 (0) | 1.30 (0.105) | 2.60 (0.156) |
| CLST | 10.72 (1.084) | 40.24 (2.820) | 12.47 (0.589) | 1.94 (0.250) | 2.00 (0) | 2.47 (0.266) |
| CLST | 8.15 (0.701) | 40.80 (2.106) | 13.65 (0.617) | 1 (0) | 1.60 (0.112) | 1.59 (0.072) |
| CLST | 12.45 (0.822) | 46.35 (1.936) | 13.10 (0.475) | 2.1 (0.228) | 1 (0) | 2.78 (0.216) |
| CLRH | JCTH | 16.45 (1.16) | 57.05 (3.237) | 15.90 (0.994) | 3.76 (0.123) | 5.93 (0.532) |
| CLRH | GANS | 14.12 (1.150) | 49.00 (2.650) | 15.35 (0.813) | 3.75 (0.106) | 5.28 (0.392) |
| ST/RH | WATS | 21.60 (0.933) | 69.25 (2.076) | 19.55 (0.709) | 1.50 (0.199) | 6.20 (0.260) |
| ST/RH | HRIM | 7.69 (0.583) | 31.88 (1.560) | 9.88 (0.554) | 2.13 (0.155) | 1.91 (0.131) |
| CLMI | WATM | 11.30 (0.821) | 50.10 (2.376) | 17.45 (1.150) | 5 (0) | 3.25 (0.160) |

TABLE 4. MULTIPLE LINEAR REGRESSION FOR ALL STUDY POPULATIONS. N = 210, R = 0.828, standard error of estimate = 0.659. Dependent variable = petal speckling.

| | Coefficient | SE | P | | |
|----------------------|-------------|--------|--------|--------|--------|
| Total petal length | 0.298 | 0.080 | <0.001 | | |
| Claw width | −0.598 | 0.214 | 0.006 | | |
| Isthmus width | 0.656 | 0.298 | 0.029 | | |
| Leaf length | −0.034 | 0.012 | 0.006 | | |
| Pollen color | 0.208 | 0.051 | <0.001 | | |
| Plant height | 0.215 | 0.043 | <0.001 | | |
| Analysis of Variance | | | | | |
| | df | SS | MS | F | P |
| Regression | 10 | 262.96 | 26.30 | 60.600 | <0.001 |
| Residuals | 199 | 86.35 | 0.43 | | |
| Total | 209 | 349.31 | 1.67 | | |

width, claw length, and isthmus width (Appendix 1); between *C. stellata* and *C. mildrediae* for all characters except petiole length, leaf length, and plant height; and between *C. rhomboidea* and *C. mildrediae* for all characters except leaf length, leaf width, pollen color, and petal speckling. Populations that were ambiguously identified as “*C. stellata*/*C. rhomboidea*” showed significant differences with *C. stellata* for limb width and total petal length; with *C. rhomboidea* for limb width, total petal length, pollen color, petal speckling, and plant height; and with *C. mildrediae* for limb width, total petal length, claw width, claw length, isthmus width, pollen color, and petal speckling (Appendix 1). Uneven sample numbers, unequal variances, and non-normal data prevented an analysis of population-by-population differences.

A multiple linear regression with petal speckling as the dependent variable indicates there is a strong correlation with this trait and the independent variables, total petal length, claw width, isthmus width, pollen color, leaf length, and plant height (Table 4).

Genetic Analysis

Two primer combinations in the AFLP process yielded a total of 136 AFLP loci among 107 individuals. Mean total heterozygosity across all pop-

ulations was 0.154 and ranged from 0.103 (GANS/CLRH) to 0.185 (JCTH/CLRH) within populations (Table 5).

An analysis of molecular variance (AMOVA) shows that although there was genetic variation among the populations (13.19%), the majority of variation is found within populations (86.81%). Genetic differentiation among all populations was also low as calculated by Genetic Data Analysis (Φ_{st} = 0.132). Variance within populations was high 32.645 (sigma-G) and variance between populations (sigma-P) was 4.96.

Based on the 136 polymorphic loci across these nine populations, the Hickory analysis revealed similar $f = 0$ and full model DIC values of 3645.59 and 3642.35, respectively and provide weak evidence for inbreeding. Comparatively, a DIC value of 3665.0 from the $\theta = 0$ model indicates there is evidence for some differentiation among populations. The f -free model in Hickory gave a $\theta^B = 0.0137$ (the Bayesian analog of G_{ST}) based on a mean f value of 0.5025 and a 95% credible interval of 0.2906 and 0.9811. The $\theta^B = 0.0137$ value is lower than traditional estimates of F_{ST} or G_{ST} because they assume total inbreeding or total outbreeding.

Distance matrix calculations and the corresponding neighbor joining tree indicate that populations consistently most closely related are: JCTH/r, MONT/s, CALF/s; CONE/s, WATM/m, GANS/r; and WILL/s, WATS/sr, HRIM/sr (Table 6, Fig. 1). A Neighbor-Joining phylogram was consistent with the AMOVA, Φ_{ST} , and Hickory data; there was no statistical significant clustering of any of the populations by initial species categorization (Fig. 1).

DISCUSSION

The purpose of this study was to determine whether there are a suite of characteristics that could be used to identify *C. stellata* from the sympatric species, *C. rhomboidea* and *C. mildrediae*, and if these characters were associated with measurable molecular variation. We have demonstrated

TABLE 5. WITHIN POPULATION STATISTICS CALCULATED USING GENETIC DATA ANALYSIS (LEWIS AND ZAYKIN, 2002). P = polymorphic loci. He = Expected heterozygosity.

| Population | n | P | He |
|------------|----|-------|-------|
| MONT/CLST | 15 | 0.577 | 0.166 |
| CALF/CLST | 6 | 0.342 | 0.123 |
| WILL/CLST | 16 | 0.592 | 0.194 |
| CONE/CLST | 14 | 0.612 | 0.158 |
| WATS/STRH | 19 | 0.622 | 0.181 |
| HRIM/STRH | 6 | 0.362 | 0.135 |
| JCTH/CLRH | 6 | 0.464 | 0.185 |
| GANS/CLRH | 11 | 0.398 | 0.103 |
| WATM/CLMI | 14 | 0.571 | 0.142 |
| Mean | 11 | 0.50 | 0.154 |

TABLE 6. DISTANCE MATRIX FOR NINE POPULATIONS BASED ON 136 AFLP LOCI USING PAUP 4b8 (SWOFFORD 2001). Nei (1978) identify above diagonal, coancestry distance below diagonal. See Table 1 for population labels. s = *stellata*, r = *rhomboidea*, sr = “*stellata/rhomboidea*”, m = *mildrediae*.

| Distance matrix | JCTH/r | MONT/s | CALF/s | WILL/s | WATS/sr | HRIM/sr | CONE/s | GANS/r | WATM/m |
|-----------------|--------|--------|--------|--------|---------|---------|--------|--------|--------|
| JCTH/r | | 0.978 | 0.962 | 0.936 | 0.921 | 0.944 | 0.948 | 0.951 | 0.957 |
| MONT/s | 0.041 | | 0.973 | 0.952 | 0.943 | 0.964 | 0.962 | 0.967 | 0.971 |
| CALF/s | 0.098 | 0.072 | | 0.960 | 0.945 | 0.965 | 0.971 | 0.976 | 0.974 |
| WILL/s | 0.181 | 0.163 | 0.111 | | 0.981 | 0.977 | 0.955 | 0.954 | 0.959 |
| WATS/sr | 0.250 | 0.208 | 0.185 | 0.051 | | 0.971 | 0.945 | 0.948 | 0.951 |
| HRIM/sr | 0.163 | 0.115 | 0.115 | 0.035 | 0.072 | | 0.956 | 0.964 | 0.964 |
| CONE/s | 0.171 | 0.141 | 0.088 | 0.156 | 0.205 | 0.157 | | 0.986 | 0.988 |
| GANS/r | 0.221 | 0.145 | 0.108 | 0.186 | 0.221 | 0.183 | 0.045 | | 0.989 |
| WATM/m | 0.153 | 0.113 | 0.086 | 0.151 | 0.191 | 0.136 | 0.029 | 0.034 | |

that populations of *C. stellata* can be separated from *C. rhomboidea* based on all vegetative characteristics measured and all floral characteristics except claw width, claw length, and isthmus width. *Clarkia mildrediae* is easily differentiated from *C. stellata* for every character except leaf length, petiole length, and plant height; *C. mildrediae* differs from *C. rhomboidea* for all characters except petal speckling, pollen color, leaf width, and leaf length. Populations that were initially difficult to categorize as either *C. stellata* or *C. rhomboidea* were most similar to *C. stellata*; however, we were not able to identify a suite of characters that would distinguish these populations as either *C. stellata* or *C. rhomboidea*. Petal speckling can be predicted from a linear combination of the independent variables, total petal length, claw width, isthmus width, pollen color, leaf length, and plant height and these correlated characters may be interpreted to be a good suite of traits with which to identify species. This correla-

tion, however, could simply mean that these characters are genetically linked regardless of species identification. Common garden experiments are needed for these taxa for further clarification on the inheritance and variability of these traits.

The analyses of molecular data indicate that most of the variation in the populations sampled is distributed across all populations. Species categorization is not consistent with the genetic data, and thus a conclusive determination about the evolutionary relationships among these populations cannot be determined here. Our data are consistent with genetic variation found in *Clarkia australis* and *C. virgata* with allozymes (Gottlieb and Ford 1999) and the high levels of allozyme variability found in *Clarkia dudleyana* that is not correlated with morphology (Podolsky 2001).

The distribution of molecular variation we found among these populations reflects shared variation between the study populations and is consistent

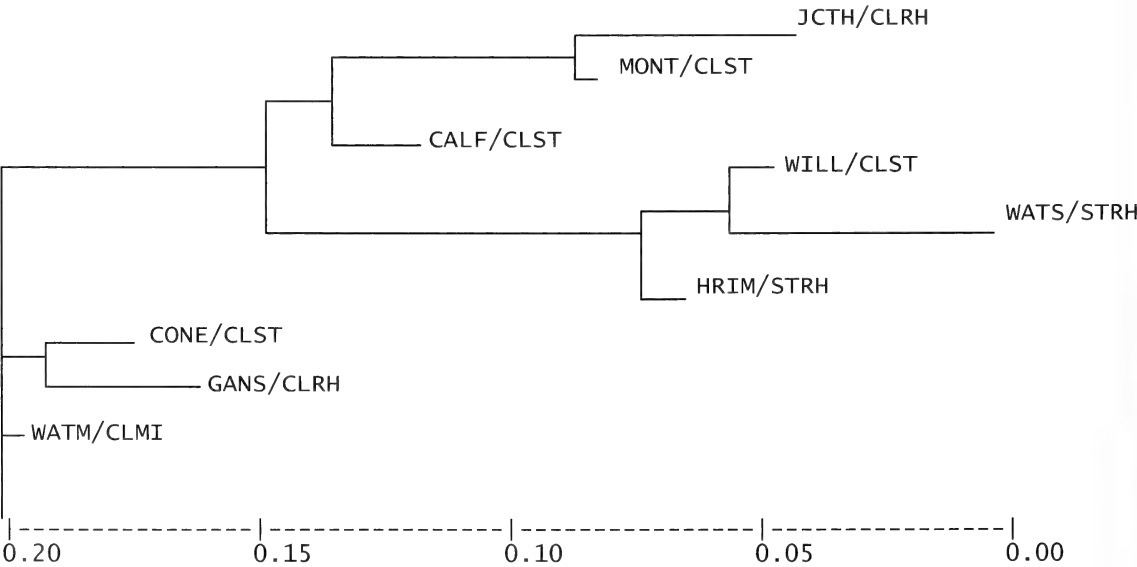


FIG. 1. Neighbor-joining tree for *C. stellata*, *C. rhomboidea*, and *C. “stellata/rhomboidea”*, *C. mildrediae* populations showing genetic distances as measured by Saitou and Nei (1987). Species and location labels are referenced in Table 2.

with the derivation of *Clarkia stellata* from *C. mildrediae*, and *C. rhomboidea* from *C. mildrediae* and *C. virgata* (Gottlieb and Janeway 1997). We cannot conclude from these data that these populations represent different species. However, AFLPs are highly variable markers (Garcia-Mas et al. 2000), and additional techniques may provide a more precise estimate of relatedness among these populations. Although the possibility exists that same-sized AFLP fragments are not homologous across species, the close relatedness and recent evolution of these species should make a lack of homology unlikely. Additionally useful tools include restriction site analysis of the inter-transcribed spacer region of rDNA (ITS) or of non-coding regions of the chloroplast genome (cpDNA). Karyotype analysis within and among populations also may clarify the evolutionary relationships among these taxa. It is imperative if either ITS or cpDNA data are collected that a number of individuals are collected from each population. Rapid evolution within and hybridization among *Clarkia* species may otherwise obscure important differences in ambiguously identified populations.

We suggest that future genetic studies include more species and populations within *Clarkia* Section *Myxocarpa*. Field identification however, may never be simplified within *Clarkia* section *Myxocarpa*. A number of studies of this section have identified taxonomic difficulties due to recent speciation, local adaptation, rapid chromosomal evolution, sympatry, and hybridization (Mosquin 1966; Small 1971a, b; Grant 1981; Gottlieb 1995; Gottlieb and Ford 1999).

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APPENDIX 1. KRUSKAL-WALLIS ONE WAY ANALYSIS OF VARIANCE ON RANKS AND ALL PAIRWISE MULTIPLE COMPARISON PROCEDURE (DUNN'S METHOD) FOR *CLARKIA STELLATA* (CLST), *C. RHOMBOIDEA* (CLRH), *C. STELLATA/RHOMBOIDEA* (STRH), AND *C. MILDREDIAE* (CLMI) POPULATIONS. Total petal length data were normally distributed ($P > 0.200$) with equal variances ($P = 0.012$) and were tested using a standard ANOVA.

Total petal length

| Group | N | Mean | SD | SE |
|-------|-----|--------|-------|--------|
| CLST | 100 | 7.054 | 0.785 | 0.0785 |
| STRH | 53 | 7.785 | 0.890 | 0.122 |
| CLRH | 37 | 9.786 | 1.307 | 0.215 |
| CLMI | 20 | 17.705 | 1.111 | 0.248 |

| Source of variation | df | SS | MS | F | P |
|---------------------|-----|---------|--------|--------|--------|
| Between species | 3 | 1980.54 | 660.18 | 726.37 | <0.001 |
| Residual | 206 | 187.23 | 0.91 | | |
| Total | 209 | 2167.77 | | | |

All pairwise multiple comparison procedures (Tukey Test)

| | Diff. of means | P value |
|---------------|----------------|---------|
| CLMI vs. CLST | 10.651 | <0.001 |
| CLMI vs. STRH | 9.920 | <0.001 |
| CLMI vs. CLRH | 7.919 | <0.001 |
| CLRH vs. CLST | 2.732 | <0.001 |
| CLRH vs. STRH | 2.002 | <0.001 |
| STRH vs. CLST | 0.731 | <0.001 |

Claw width

| Species | N | Median | 25% | 75% |
|---------|-----|--------|-------|-------|
| CLST | 100 | 2.00 | 1.900 | 2.200 |
| STRH | 53 | 2.00 | 1.600 | 2.425 |
| CLRH | 37 | 2.00 | 1.900 | 2.400 |
| CLMI | 20 | 3.95 | 3.750 | 4.300 |

H = 55.362, df = 3, P = < 0.001

| Comparison | Diff. of ranks | Q value | P < 0.05 |
|---------------|----------------|---------|----------|
| CLMI vs. STRH | 108.340 | 6.794 | Yes |
| CLMI vs. CLST | 106.320 | 7.143 | Yes |
| CLMI vs. CLRH | 96.649 | 5.731 | Yes |
| CLRH vs. STRH | 11.691 | 0.898 | No |
| CLRH vs. CLST | 9.671 | 0.827 | No |
| CLST vs. STRH | 2.020 | 0.196 | No |

Claw length

| Species | N | Median | 25% | 75% |
|---------|-----|--------|-------|-------|
| CLST | 100 | 1.500 | 1.300 | 1.600 |
| STRH | 53 | 1.600 | 1.500 | 1.825 |
| CLRH | 37 | 2.200 | 1.700 | 2.525 |
| CLMI | 20 | 4.000 | 3.650 | 4.400 |

H = 108.708, df = 3, P = < 0.001.

| Comparison | Diff. of ranks | Q value | P < 0.05 |
|---------------|----------------|---------|----------|
| CLMI vs. STRH | 131.060 | 8.805 | Yes |
| CLMI vs. CLST | 96.519 | 6.053 | Yes |
| CLMI vs. CLRH | 96.649 | 2.770 | Yes |
| CLRH vs. STRH | 11.691 | 7.213 | No |
| CLRH vs. CLST | 9.671 | 3.826 | No |
| CLST vs. STRH | 2.020 | 3.346 | No |

APPENDIX 1. CONTINUED.

Isthmus width

| Species | N | Median | 25% | 75% |
|---------|-----|--------|-------|-------|
| CLST | 100 | 1.700 | 1.600 | 1.800 |
| STRH | 53 | 1.800 | 1.500 | 1.925 |
| CLRH | 37 | 1.800 | 1.600 | 2.000 |
| CLMI | 20 | 2.900 | 2.600 | 3.100 |

H = 63.122, df = 3, P < 0.001.

| Comparison | Diff. of ranks | Q value | P < 0.05 |
|---------------|----------------|---------|----------|
| CLMI vs. CLST | 116.395 | 7.820 | Yes |
| CLMI vs. STRH | 95.520 | 5.990 | Yes |
| CLMI vs. CLRH | 86.931 | 5.155 | Yes |
| CLRH vs. CLST | 29.464 | 2.520 | No |
| CLRH vs. STRH | 8.589 | 0.660 | No |
| STRH vs. CLST | 20.875 | 2.002 | No |

Limb width

| Species | N | Median | 25% | 75% |
|---------|-----|--------|--------|--------|
| CLST | 100 | 4.100 | 3.700 | 4.500 |
| STRH | 53 | 4.700 | 4.100 | 5.000 |
| CLRH | 37 | 5.200 | 4.675 | 5.725 |
| CLMI | 20 | 12.650 | 11.900 | 12.950 |

H = 98.685, df = 3, P < 0.001.

| Comparison | Diff. of ranks | Q value | P < 0.05 |
|---------------|----------------|---------|----------|
| CLMI vs. CLST | 130.375 | 8.759 | Yes |
| CLMI vs. STRH | 91.660 | 5.748 | Yes |
| CLMI vs. CLRH | 55.527 | 3.292 | Yes |
| CLRH vs. CLST | 74.848 | 6.401 | Yes |
| CLRH vs. STRH | 36.133 | 2.776 | Yes |
| STRH vs. CLST | 38.715 | 3.750 | Yes |

Petiole length

| Species | N | Median | 25% | 75% |
|---------|-----|--------|--------|--------|
| CLST | 100 | 11.000 | 9.000 | 15.000 |
| STRH | 53 | 11.000 | 8.000 | 19.000 |
| CLRH | 37 | 16.000 | 11.000 | 19.000 |
| CLMI | 20 | 11.000 | 8.000 | 13.500 |

H = 11.672, df = 3, P = 0.009.

| Comparison | Diff. of ranks | Q value | P < 0.05 |
|---------------|----------------|---------|----------|
| CLRH vs. CLMI | 45.080 | 2.673 | Yes |
| CLRH vs. CLST | 36.605 | 3.131 | Yes |
| CLRH vs. STRH | 24.490 | 1.881 | No |
| STRH vs. CLMI | 20.590 | 1.291 | No |
| STRH vs. CLST | 12.115 | 1.173 | No |
| CLST vs. CLMI | 8.475 | 0.569 | No |

Leaf length

| Species | N | Median | 25% | 75% |
|---------|-----|--------|--------|--------|
| CLST | 100 | 44.000 | 38.500 | 52.000 |
| STRH | 53 | 43.000 | 32.750 | 64.250 |
| CLRH | 37 | 53.000 | 44.000 | 63.500 |
| CLMI | 20 | 48.000 | 42.500 | 57.500 |

H = 8.949, df = 3, P = 0.030.

APPENDIX 1. CONTINUED.

| Comparison | Diff. of ranks | Q value | P < 0.05 |
|---------------|----------------|---------|----------|
| CLRH vs. CLST | 32.970 | 2.820 | Yes |
| CLRH vs. STRH | 25.531 | 1.961 | No |
| CLRH vs. CLMI | 10.410 | 0.617 | No |
| CLMI vs. CLST | 22.560 | 1.516 | No |
| CLMI vs. STRH | 15.121 | 0.948 | No |
| STRH vs. CLST | 7.439 | 0.720 | No |

Leaf width

| Species | N | Median | 25% | 75% |
|---------|-----|--------|--------|--------|
| CLST | 100 | 13.000 | 11.000 | 15.000 |
| STRH | 53 | 14.000 | 10.750 | 18.000 |
| CLRH | 37 | 15.000 | 13.000 | 18.250 |
| CLMI | 20 | 16.500 | 14.500 | 20.000 |

H = 20.331, df = 3, P < 0.001.

| Comparison | Diff. of ranks | Q value | P < 0.05 |
|---------------|----------------|---------|----------|
| CLMI vs. CLST | 5.315 | 3.716 | Yes |
| CLMI vs. STRH | 41.344 | 2.593 | No |
| CLMI vs. CLRH | 17.311 | 1.026 | No |
| CLRH vs. CLST | 38.004 | 3.250 | Yes |
| CLRH vs. STRH | 24.032 | 1.846 | No |
| STRH vs. CLST | 13.971 | 1.353 | No |

Pollen color

| Species | N | Median | 25% | 75% |
|---------|-----|--------|-------|-------|
| CLST | 100 | 3.000 | 1.000 | 3.000 |
| STRH | 53 | 3.000 | 3.000 | 3.000 |
| CLRH | 37 | 5.000 | 5.000 | 5.000 |
| CLMI | 20 | 5.000 | 5.000 | 5.000 |

H = 139.364, df = 3, p < 0.001.

All pairwise multiple comparison procedures
(Dunn's Method)

| | Diff. of ranks | Q value | P < 0.05 |
|---------------|----------------|---------|----------|
| CLMI vs. CLST | 114.465 | 7.690 | Yes |
| CLMI vs. STRH | 89.330 | 5.602 | Yes |
| CLMI vs. CLRH | 68.216 | 0.487 | No |
| CLRH vs. CLST | 106.249 | 9.087 | Yes |
| CLRH vs. STRH | 81.114 | 6.231 | Yes |
| STRH vs. CLST | 25.135 | 2.434 | No |

Petal speckling

| Species | N | Median | 25% | 75% |
|---------|-----|--------|-------|-------|
| CLST | 100 | 2.000 | 1.000 | 2.000 |
| STRH | 53 | 2.000 | 2.000 | 2.000 |
| CLRH | 37 | 4.000 | 3.000 | 4.000 |
| CLMI | 20 | 5.000 | 5.000 | 5.000 |

H = 148.086, df = 3, P < 0.001.

| Comparison | Diff. of ranks | Q value | P < 0.05 |
|---------------|----------------|---------|----------|
| CLMI vs. CLST | 131.400 | 8.828 | Yes |
| CLMI vs. STRH | 106.774 | 6.696 | Yes |
| CLMI vs. CLRH | 28.270 | 1.676 | No |
| CLRH vs. CLST | 103.130 | 8.820 | Yes |
| CLRH vs. STRH | 78.503 | 6.030 | Yes |
| STRH vs. CLST | 24.626 | 2.385 | No |

APPENDIX 1. CONTINUED.

| Plant height | | | | |
|--------------------------------|-----|--------|-------|-------|
| Species | N | Median | 25% | 75% |
| CLST | 100 | 3.000 | 2.000 | 4.250 |
| STRH | 53 | 2.500 | 2.000 | 5.625 |
| CLRH | 37 | 5.500 | 4.000 | 7.000 |
| CLMI | 20 | 3.000 | 3.000 | 3.500 |
| H = 36.560, df = 3, P < 0.001. | | | | |

| Comparison | Diff. of ranks | Q value | P < 0.05 |
|---------------|----------------|---------|----------|
| CLRH vs. CLST | 69.606 | 5.953 | Yes |
| CLRH vs. STRH | 58.682 | 4.508 | Yes |
| CLRH vs. CLMI | 58.641 | 3.477 | Yes |
| CLMI vs. CLST | 10.965 | 0.737 | No |
| CLMI vs. STRH | 0.042 | 0.003 | No |
| STRH vs. CLST | 10.923 | 1.058 | No |

INFLUENCE OF PLANT SIZE AND CLIMATIC VARIABILITY ON THE FLORAL BIOLOGY OF *FOUQUIERIA SPLENDENS* (OCOTILLO)

JANICE E. BOWERS

U.S. Geological Survey, 1675 W. Anklam Rd., Tucson, AZ 85745

jebowers@usgs.gov

ABSTRACT

The floral biology of *Fouquieria splendens* (Fouquieriaceae), a drought-deciduous shrub with wandlike branches, was studied in the northern Sonoran Desert. Two different measures of plant size, number of branches long enough to flower (>1 m in length) and actual number of reproductive branches, were used to examine the effect of plant size on reproductive output and floral display. Number of flowers and fruits increased with either measure of plant size. Annual flower production ranged from 190 to 6465 per plant and averaged 2553. Annual fruit production ranged from 9 to 1760 per plant and averaged 390. Because some branches long enough to flower did not do so, number of reproductive branches was a stronger predictor of flower production than number of branches > 1 m long. Inflorescence size (mean number of flowers per panicle) was not significantly related to plant size (number of flowering branches) in 2002 or 2003; in fact, the range in inflorescence size on certain individual plants was about as wide as the range for the entire sample. Interannual variation in floral parameters was examined by monitoring the same set of branches in two years, one unusually dry, one with nearly normal rain. In 2002, the dry year, panicles were numerous and sparsely flowered; in 2003, the wetter year, panicles were relatively few and much more densely flowered. Although flowers *appeared* normally abundant in the wetter year, mean number of flowers per branch was in fact 39% lower than in the dry year. Percent fruit set per panicle in 2003 (36%) was more than twice that in 2002 (16%). Even so, average number of fruits per branch did not differ between 2002 and 2003. Evidently flower production on a per-branch basis was high enough in 2002 to compensate for poor fruit set in that year, resulting in about as many fruits as in 2003.

RESUMEN

La biología de las flores de *Fouquieria splendens* (Fouquieriaceae), un arbusto tolerante de sequía con ramas como varitas, fue estudiada en parte norte del desierto sonorense. Dos medidas diferentes del tamaño de la planta, el número de ramas suficiente largas para producir flores (> 1 m del largo) y el número de las ramas en realidad con flores, fueron usadas para examinar el efecto del tamaño de la planta en la producción reproductora y la exposición de las flores. El número de las flores y las frutas aumentaron con ambas medidas del tamaño de la planta. La producción anual de las flores fue entre 190 y 6465 por planta con un promedio de 2553. La producción anual de las frutas fue entre 9 y 1760 por planta con un promedio de 390. Porque algunas ramas suficiente largas para producir flores no florecieron, el número de las ramas en realidad con flores fue mejor que el número de las ramas más largas de un metro para predecir la producción total de flores. El tamaño de la inflorescencia (el número promedio de las flores por panícula) no fue correlacionado significativamente con el tamaño de la planta (como el número de las ramas con flores) en 2002 o 2003; en realidad, la variedad en el tamaño de la inflorescencia en ciertas plantas fue más o menos lo mismo que la de todos de las plantas medidas. La variación entre años en los parámetros de las flores fue estudiado por observar el grupo mismo de ramas en dos años, un año muy seco, el otro con lluvia casi normal. En 2002, el año seco, hubo muchas panículas con pocas flores; en 2003, el año con más lluvia, hubo menos panículas pero con muchas más flores por panícula. Aunque las flores parecieron normalmente abundantes en el año con más lluvia, el número promedio de flores por rama en realidad fue 39% menos que en el año seco. El porcentaje de frutas producidas por panícula en 2003 (36 %) fue más que doble lo del 2002 (16 %). Sin embargo, el número promedio de frutas por rama fue diferente entre 2002 y 2003. Obviamente la producción de flores en la base por rama fue suficiente en 2002 para compensar por la peor producción de frutas en ese año, lo que resultar en casi el mismo número de frutas como en 2003.

Key Words: floral biology, flower production, *Fouquieria splendens*, fruit production, fruit set, inter-annual variation, Sonoran Desert.

Flower and fruit production integrate a plant's physical and biological environment, serving as an assay of the combined effects of pollinator behavior, climatic variability, and resource limitation. Ecologists use estimates of flower or fruit production in quantifying the floral resources available to pollinators (e.g., Hocking 1968; Tepedino and Stan-

ton 1981); in assessing selective pressures on inflorescence architecture (e.g., Worley et al. 2000; Gal- loway et al. 2002); and in determining population growth rates and other demographic parameters (e.g., Mandujano et al. 2001). Within species, plant size can have a substantial impact on reproductive output: for the columnar cactus *Carnegiea gigantea*

(Engelm.) Britton & Rose, every additional branch has the potential to augment flower production by about 100 flowers (Steenbergh and Lowe 1977). Plant size can modulate the influence of climatic variability on annual flower production of some woody plants. In a four-year study of *Opuntia engelmannii* Salm-Dyck., for example, the number of flowers initiated by a sample of 26 plants did not vary significantly among years even though winter rain in those years ranged over an order of magnitude (Bowers 1996).

Although plant size is a crucial component of flower production, counting all flowers on large shrubs or trees is scarcely feasible for many species, leaving ecologists with no choice but to subsample, often with little or no regard to variation in plant size (e.g., Solbrig and Cantino 1975; Simpson 1977; Boyd and Brum 1983). In the Sonoran Desert, *Fouquieria splendens* Engelm. (Fouquieriaceae) is probably about as large and fecund a plant as can be conveniently assessed without subsampling. Previous studies of this species have emphasized the effect of pollinators on fruit and seed production (Waser 1979; Scott 1989) while downplaying the effect of climatic variability on flower production (Darrow 1943; Scott 1989), but none have examined the influence of plant size on reproductive output or floral display. The main objective of this study was to determine the effect of plant size on the floral biology of *F. splendens*, including annual flower and fruit production, inflorescence size, and proportion of fertile branches.

A secondary objective of this study was to examine interannual variation in floral display and reproductive output. Several observers have concluded that climatic variability has little influence on flower production in *F. splendens*, but this conclusion depends on subjective impressions (Shreve 1925; Humphrey 1975), which can be misleading, or on counts of inflorescences (Darrow 1943), which are a reliable measure of flower production only if number of flowers per inflorescence is stable from year to year. The only between-year comparison of *F. splendens* flower production (Scott 1989) found significant interannual variation at one of three Chihuahuan Desert sites; somewhat unexpectedly, plants produced more flowers after the drier winter.

In this study, I harvested and counted all flowers, inflorescences, and fruits on 10 plants in two years to determine how flower and fruit production, inflorescence size, and proportion of fertile branches vary with plant size. Because removal of all flowers or fruits could conceivably influence reproductive output in the following year, different plants were sampled in 2002 and 2003. No between-year comparisons were made with these samples. Rather, I monitored inflorescence size, inflorescence number, and fruit set on a sample of branches in an unusually dry year and in a year of nearly normal rainfall to assess the potential for interannual variation in

reproductive output. Specific questions addressed were: Does inflorescence size (number of flowers per panicle) vary from year to year and plant to plant? To what extent does plant size determine inflorescence size, inflorescence number, and reproductive output? Does plant size account for variation in the proportion of branches that reproduce each year? Is inflorescence production a reliable guide to flower production? Are flower production and fruit set independent of precipitation in the preceding year?

METHODS

Study Area

The study was conducted at Tumamoc Hill (32°13'N, 111°05'W), an outlier of the Tucson Mountains, Pima County, Arizona, USA. The study area, which encompasses about 352 ha, is owned and operated by the University of Arizona as the Desert Laboratory and is situated just west of downtown Tucson, Arizona. The Desert Laboratory grounds include Tumamoc Hill proper, a rocky, basaltic-andesitic knoll (760 to 948 m above sea level), and the level or gently rolling plain to the west (725 to 760 m above sea level). Domestic livestock have been excluded from the study site since 1907. At Tucson, rainfall averages 280 mm per year. Almost half comes during July, August, and September; most of the remainder falls between November and March (Sellers et al. 1985). Average maximum and minimum daily temperatures are 18.6°C and 2.4°C during January, the coldest month, and 37.9°C and 22.8°C in June, the hottest month (Sellers et al. 1985). Vegetation at Tumamoc Hill is typical of the Arizona Upland subdivision of the Sonoran Desert (Shreve 1951). In addition to *F. splendens*, dominant plants include *Cercidium microphyllum* (Torr.) Rose & Johnston, *Carnegiea gigantea*, *Larrea tridentata* (Sessé & Moç. ex DC.) Cov., *Ambrosia deltoidea* (A. Gray) Payne, *Acacia constricta* Benth., and *Ferocactus wislizeni* (Engelm.) Britton & Rose.

Study Species

Fouquieria splendens is a woody plant with several to 100 wandlike, ascending or erect branches that arise from a very short trunk. The species is locally common in desert scrub and grassland throughout the southwestern United States and northern Mexico (Turner et al. 1995). Branches grow in length when terminal buds elongate during the summer rainy season (Darrow 1943). In a six-year study in the vicinity of Tucson, Arizona, branches < 1 m in length elongated annually but did not flower (Darrow 1943). Mature branches, on the other hand, flowered annually and elongated but every two or three years, if at all (Darrow 1943). Throughout its range, *F. splendens* typically flowers in spring, rarely in autumn (Turner et al. 1995).

Prolonged drought (several years) can suppress flowering entirely (Carlquist 2001). The hermaphroditic, red, tubular flowers are 6 to 22 mm long and are borne in panicles of cymes near the branch tips (Henrickson 1969). Number of panicles per branch increases with branch length (Darrow 1943). Flowers can self pollinate but only to a limited extent (Waser 1979), and the breeding system is best regarded as self-incompatible (Scott 1989). On average, a mature plant annually produces about 2000 flowers (Scott et al. 1993), 200 fruits (Waser 1979), and 800 to 2200 seeds (Waser 1979). The primary pollinators are hummingbirds and carpenter bees (Waser 1979; Scott 1989; Scott et al. 1993). Scott (1989) reported natural fruit set as high as 82% from some Chihuahuan Desert sites and achieved 88% fruit set by outcrossing flowers by hand. He concluded that when pollinators are plentiful, plants have the resources to set large numbers of fruits.

Effect of Plant Size on Reproductive Output and Floral Display

Flower production was determined in April 2002 and April 2003. Different plants were sampled in successive years. In each year, 10 plants were selected to represent a range of sizes, that is, number of branches. Size of each plant was measured in two different ways: as number of potentially reproductive branches (branches > 1 m long) and as number of branches that actually reproduced (flowering branches). All panicles on each plant were removed and placed in labeled paper bags. The number of flower buds and flowers on each panicle was counted and recorded by plant; any unattached flowers in the bottom of the bag were added to the total for the plant.

To examine the influence of plant size on total flower production in each year, number of flowers per plant was used as the dependent variable in separate linear regressions against number of branches > 1 m long and against number of flowering branches. Because total flower production reflects both inflorescence production (number of panicles per plant) and inflorescence size (number of flowers per panicle), either of which might change with plant size, several more analyses were performed. To examine the influence of plant size on inflorescence production, number of panicles per plant in each year was regressed against number of flowering branches per plant. To assess whether plant size affects inflorescence size, the range in inflorescence size in 2002 and 2003 was summarized graphically by showing for each plant the largest and smallest panicles (maximum and minimum number of flowers per panicle) and the mean number of flowers per panicle. In addition, mean number of flowers per panicle was regressed against number of flowering branches per plant. Separate regressions were performed for 2002 and 2003.

These analyses used the 10-plant samples described above.

Fruit production was determined in May 2002 and May 2003. Again, 10 different plants in each year were selected to represent a range of sizes, and separate counts were made of fruiting branches and of nonfruiting branches > 1 m long. All fruiting panicles on each plant were harvested, and fruits were counted as for flowers. Number of fruits per plant was plotted as a function of number of branches > 1 m long or number of fruiting branches. In both cases, number of fruits appeared to level off as plant size increased, so nonlinear regression was used to fit a curve to the data points.

There is some between-year variation in number of branches that flower (Darrow 1943). To characterize this variation, the proportion of reproductive branches in each year was calculated for each of the 10 sample plants as number of branches in flower divided by number of branches > 1 m long. Linear regression was used to examine the effect of plant size (number of branches > 1 m) on percent of branches that flowered. Proportions were transformed for analysis using the arcsin of the square root.

Interannual Variation in Inflorescence Size, Fruit Set, and Patterns of Abortion

To assess interannual variation in inflorescence size and fruit set, 22 reproductive branches on five plants were tagged and monitored from bud stage in late March to fruit maturation in mid-May in 2002 and 2003. The same branches were monitored in both years. Numbers of flower buds, open flowers, and fruits on individual panicles were counted weekly. Sampling was non-destructive. These data were summarized such that flowering and fruiting effort could be compared between years at each of two levels, panicle and branch. At the panicle level, means for number of flowers initiated per panicle, number of fruits matured per panicle, and proportion of flowers on each panicle that set fruit were calculated for each of the five sample plants. Values for fruit set were transformed for analysis using the arcsin of the square root. Individual plant means were then compared between years using paired *t*-tests; results were reported as grand means across all five plants in 2002 or 2003. At the branch level, means for number of panicles per branch, number of flowers initiated per branch, and number of fruits matured per branch were also calculated for individual plants and compared between years using paired *t*-tests. Patterns of abortion were examined for three stages (buds, flowers, immature fruits) after summing for all 22 branches the number of structures produced in each stage in each year. Abortion was calculated within stages using the number of structures in a given stage as the denominator and number of structures in the next stage as the numerator. For example, percent of immature

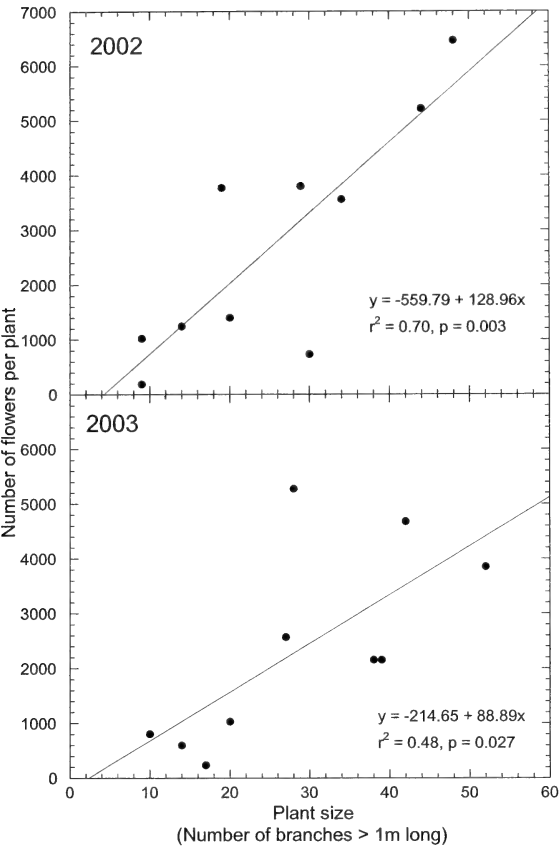


FIG. 1. Relation between plant size, measured as number of branches > 1 m long, and number of flowers in 2002 (top) and 2003 (bottom) for *Fouquieria splendens*, Tumamoc Hill, Tucson, Arizona.

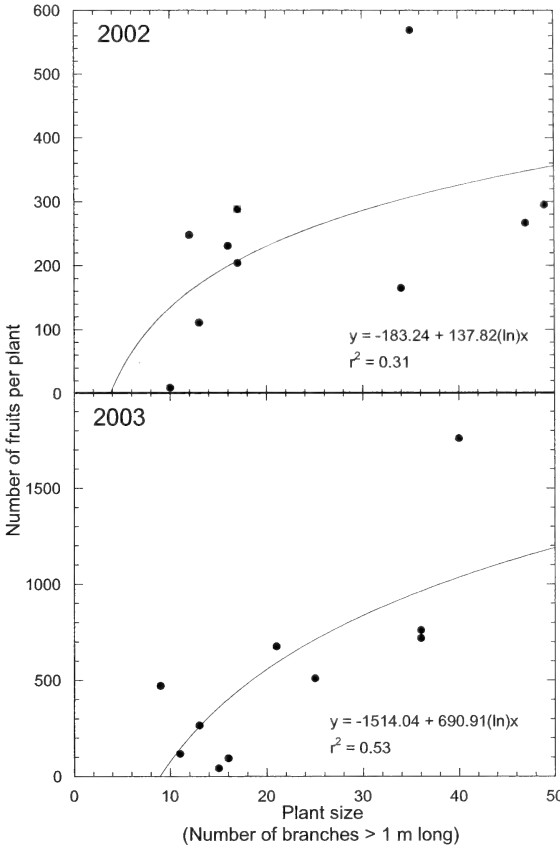


FIG. 2. Relation between plant size, measured as number of branches > 1 m long, and number of fruits in 2002 (top) and 2003 (bottom) for *Fouquieria splendens*, Tumamoc Hill, Tucson, Arizona.

fruits aborted = [1.0 - (number of mature fruits/number of immature fruits)] × 100%. Cumulative abortion was calculated for every stage by summing abortions for that stage and all previous stages, then dividing the total by number of buds.

RESULTS

Effect of Plant Size on Flower and Fruit Production

Flower and fruit production were close to previous estimates (Waser 1979; Scott 1989). When years were pooled (n = 20 plants), there were on average 2553 ± 1942 flowers per plant and 390 ± 394 fruits per plant. (All means are reported as ± 1 SD.) Number of flowers and number of fruits increased with number of branches > 1 m in length. The relation was linear for flowers (Fig. 1) but appeared to be logarithmic for fruits (Fig. 2). The effect of plant size on reproductive output was even stronger when number of flowering or fruiting branches was used as the independent variable. Again, the relation was linear for flowers (Fig. 3), logarithmic for fruits (Fig. 4). Not all branches

large enough to flower (>1 m in length) did so: in 2002 and 2003, respectively, the proportion of branches in flower averaged 76% (range = 37% to 100%) and 63% (12% to 80%). The proportion of reproductive branches was independent of plant size (number of branches > 1 m) in both 2002 and 2003 (Fig. 5).

Effect of Plant Size on Inflorescence Production and Inflorescence Size

Inflorescence production (number of panicles per plant) increased linearly with plant size in 2002 and 2003 (Fig. 6). Inflorescence size (number of flowers per panicle), however, appeared to be little affected by plant size. In both years, the range in inflorescence size on certain individual plants was about as wide as the range for the entire 10-plant sample (Fig. 7). In 2002, for example, one plant produced panicles with as few as eight flowers and as many as 182; the range for all 10 plants that year was a minimum of eight and a maximum of 192. The difference between the smallest and largest panicles on a plant typically spanned an order of magnitude (Fig. 7). Inflorescence size (mean number of flow-

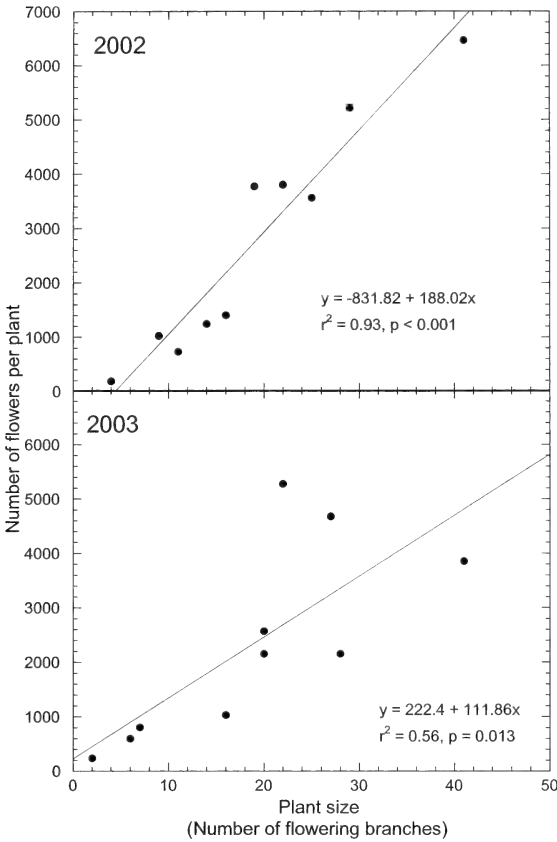


FIG. 3. Relation between plant size, measured as number of flowering branches, and number of flowers in 2002 (top) and 2003 (bottom) for *Fouquieria splendens*, Tumamoc Hill, Tucson, Arizona.

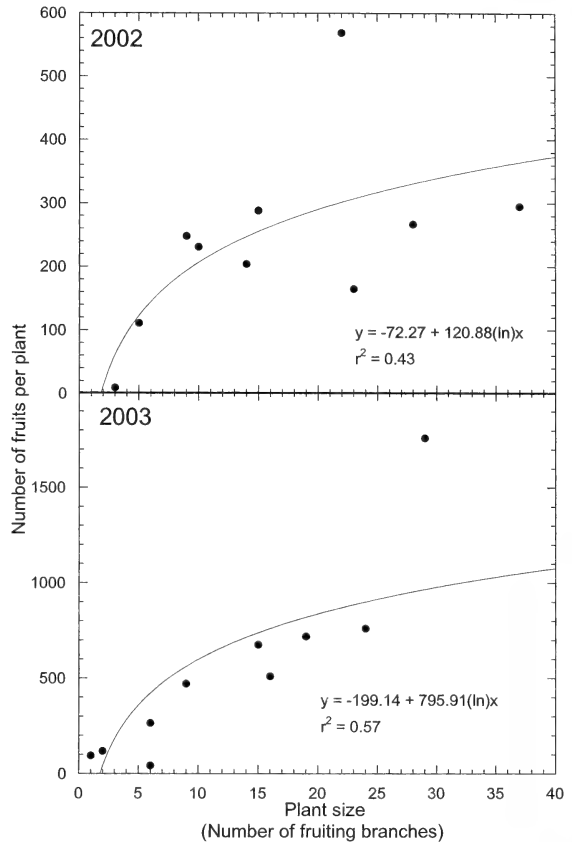


FIG. 4. Relation between plant size, measured as number of fruiting branches, and number of fruits in 2002 (top) and 2003 (bottom) for *Fouquieria splendens*, Tumamoc Hill, Tucson, Arizona.

ers per panicle) was not significantly related to plant size (number of flowering branches) in 2002 ($r^2 = 0.36$, $P = 0.07$) or 2003 ($r^2 = 0.09$, $P = 0.40$).

Interannual Variability in Inflorescence Size, Fruit Set, and Abortion

The 22 tagged branches monitored in two successive years showed marked interannual variability in flower production. The grand mean across five plants was 103 ± 13.0 flowers per branch in 2002 and 63 ± 18.6 flowers per branch in 2003, a significant difference ($t = 5.9$, $P = 0.004$). Reproductive display differed between years as well. Specifically, branches produced many few-flowered panicles in 2002 as opposed to a small number of many-flowered panicles in 2003. The grand mean for number of panicles per branch was 6 ± 1.8 in 2002 and 1 ± 0.3 in 2003, a significant difference ($t = 3.6$, $P = 0.02$). In 2002, five plants averaged 21 ± 6.6 flowers per panicle; in 2003, the average was 59 ± 15.9 . Again, means differed significantly between years ($t = 7.2$, $P = 0.002$). Averaged across five plants, fruit set per panicle in 2003 ($36\% \pm 0.1\%$) was about twice that in 2002 ($16\% \pm$

0.1%), but the difference was not significant ($t = 2.5$, $P = 0.07$). Even so, actual number of fruits was significantly lower in 2002 than in 2003 ($t = 5.5$, $P = 0.005$). Specifically, in 2002 the grand mean was 4 ± 2.3 fruits per panicle, whereas in 2003 it was 25 ± 7.5 fruits per panicle. Grand means for number of fruits per branch did not differ between 2002 (19 ± 12.9) and 2003 (26 ± 9.5) ($t = 0.7$, $P = 0.51$).

Patterns of bud, flower, and immature fruit abortion differed somewhat between years on the 22 tagged branches. Table 1 shows percent abortion in each stage (flower bud, flower, immature fruit) and cumulative abortion for the entire flowering season. In 2002, percent abortion was highest in the bud (42%) and immature fruit stages (63%), lowest in the flower stage (22%). In 2003, percent abortion was again highest for buds (50%) whereas approximately equal proportions of flowers (14%) and immature fruits (18%) aborted. Patterns of cumulative abortion were similar between years in the early stages, with 55% and 57% cumulative abortion of buds and flowers in 2002 and 2003, respectively (Table 1). Not until the immature fruit stage was

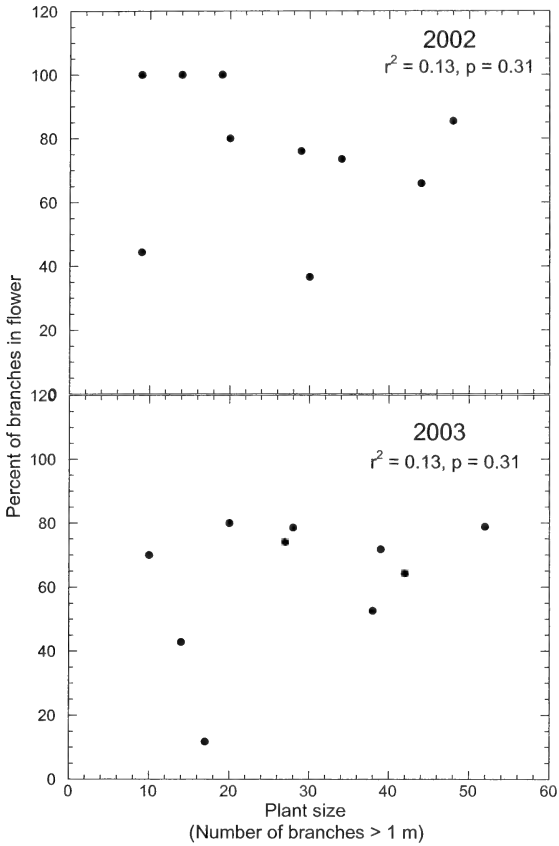


FIG. 5. Relation between plant size, measured as number of branches > 1 m long, and proportion of branches that flowered in 2002 (top) and 2003 (bottom) for *Fouquieria splendens*, Tumamoc Hill, Tucson, Arizona.

there a marked difference between years: the total proportion of structures aborted was 83% in 2002 compared to 65% in 2003 (Table 1).

DISCUSSION

Annual flower production of *Fouquieria splendens* increased linearly with plant size, whether measured as number of potentially reproductive branches (all branches > 1 m in length) (Fig. 1) or as number of branches that actually reproduced (all flowering branches) (Fig. 3). It appeared that the increase in flower production with plant size was a function of more panicles rather than larger panicles (Figs. 6, 7). Although branches > 1 m are large enough to flower, not all do so annually (Darrow 1943); during this study, the proportion of flowering branches per plant ranged from 12% to 100% and averaged 69%. The proportion was independent of plant size (Fig. 5). As for vegetative growth (Darrow 1943), whether a particular branch reproduces in a given year might depend on a complicated combination of seasonal precipitation, branch length, and activity in previous years. Because some branches > 1 m long failed to flower, the

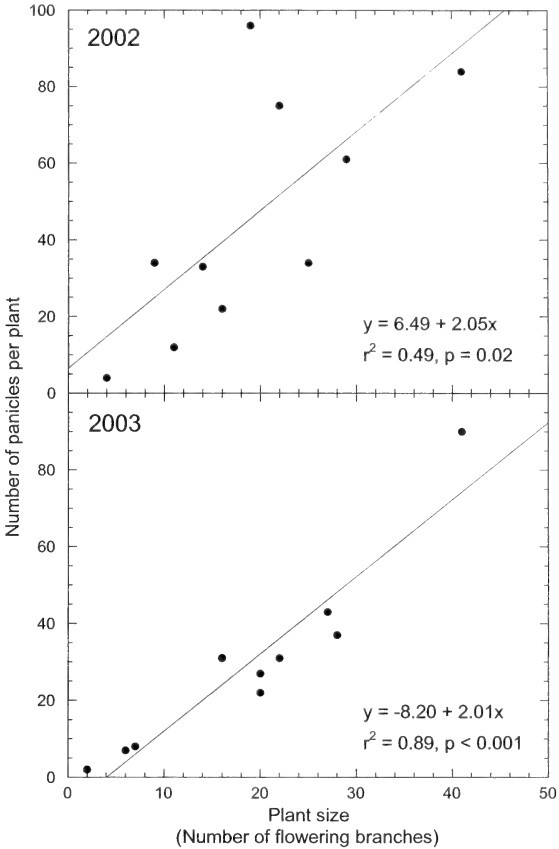


FIG. 6. Relation between plant size, measured as number of flowering branches, and inflorescence production, measured as number of panicles per plant, in 2002 (top) and 2003 (bottom) for *Fouquieria splendens*, Tumamoc Hill, Tucson, Arizona.

number of reproductive branches was a stronger predictor of flower production than number of branches > 1 m long.

There was considerable variation among plants in maximum and mean number of flowers per panicle (Fig. 7), but the variation could not be ascribed to plant size, probably because variation among branches on a single plant overwhelmed any differences between plants. Specifically, long branches produce more inflorescences (Darrow 1943) and larger inflorescences (Bowers, unpublished data) than short branches. Except for very small and very large individuals, most plants have both short and long branches, thus both small and large panicles. Because panicles of all sizes can be found on most plants, there is no relation between plant size and inflorescence size. Insofar as panicle size and number vary with branch length, annual flower production should be more strongly related to the sum of individual branch lengths than to number of branches in flower. However, the difficulty of measuring thorny branches up to 5 m in length makes number of branches a useful proxy.

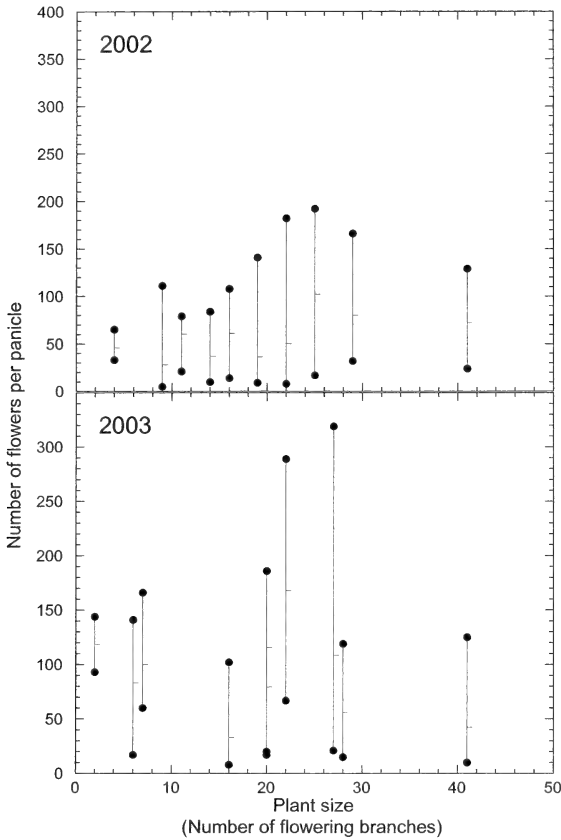


FIG. 7. Between-plant variation in inflorescence size in 2002 (top) and 2003 (bottom) for *Fouquieria splendens*, Tumamoc Hill, Tucson, Arizona. Circles show largest and smallest panicles on each plant (maximum and minimum number of flowers per panicle). Ticks show mean number of flowers per panicle. X axis shows plant size, measured as number of flowering branches.

Fruit production, like flower production, increased with plant size and ranged from 9 to 1760 fruits per plant per year (Figs. 2, 4). The relation between plant size and number of fruits was logarithmic, indicating that plants of moderate to large size tended to abort a higher proportion of flowers than small plants. Higher levels of abortion on large plants might reflect increasing inefficiency of pollen transfer as pollinators move among the many

inflorescences on a large plant. Pollen is clearly not the only factor that limits fruit production, however; 42% to 50% of abortions took place during the bud stage (Table 1). Resources available to a plant for a given flowering episode might limit the number of buds that develop into flowers; if the effect becomes stronger as plants increase in size, large plants might set no more fruits than moderate-sized plants. Conceivably, both resources and pollen limit fruit production as plants grow (e.g., Campbell and Halama 1993).

Darrow (1943) used number of inflorescences per plant as a measure of flower production in *F. splendens*. Although it is easier to count inflorescences than individual flowers, inflorescence counts can be misleading when comparing flower production among years. Close monitoring of the same set of 22 branches showed that floral parameters differed significantly in two consecutive years. In 2002, panicles were numerous and sparsely flowered; in 2003, panicles were relatively few and much more densely flowered. Although flowers appeared normally abundant in 2003, mean number of flowers per branch was in fact 39% lower than in the previous year.

A two-year study is not long enough to determine how reproductive output varies with precipitation, but because of marked differences in seasonal rain between the two years, it is tempting to draw some tentative conclusions. Before the 2002 flowering season, winter-spring (November to April) rain was just 26.2 mm. The 2003 flowering season followed a winter-spring of nearly normal rainfall, 68.1 mm. Number of flowers per branch was 103 in 2002, 63 in 2003. Thus, a 2-fold increase in flower production was accompanied by a 3-fold decrease in rain. In 1987 and 1988, Scott (1989) similarly found a 2-fold increase in flowers per plant with a 4-fold decrease in winter-spring rain. Although the difference between years in rain was relatively large in both studies, the difference between years in number of flowers was relatively modest. It is worth noting that the winter-spring of 2001–2002 was the driest on record at the study site, and several woody species failed to bloom in spring 2002, among them a shrubby tree (*Cercidium microphyllum*), a small shrub (*Ambrosia deltoidea*), and a cactus (*Opuntia engelmannii*) (pers.

TABLE 1. PATTERNS OF *FOUQUIERIA SPLENDENS* BUD, FLOWER, AND FRUIT ABORTION ON 22 BRANCHES IN TWO YEARS AT TUMAMOC HILL, TUCSON, ARIZONA.

| | Number produced | 2002 | | Number produced | 2003 | |
|-----------------|--------------------|-----------------|------------|--------------------|-----------------|------------|
| | | Percent aborted | | | Percent aborted | |
| | | Stage | Cumulative | | Stage | Cumulative |
| Buds | 2264 | 42 | 42 | 1623 | 50 | 50 |
| Flowers | 1319 | 22 | 55 | 817 | 14 | 57 |
| Immature fruits | 1025 | 63 | 83 | 700 | 18 | 65 |
| Mature fruits | 382 | — | — | 572 | — | — |

obs.). Remarkably, *F. splendens* not only bloomed in 2002 but apparently bloomed heavily. Either flower production in this species is not greatly influenced by rain (Shreve 1925; Darrow 1943; Humphrey 1975; Scott 1989), or some other measure of precipitation is more pertinent.

In contrast to flower production, percent fruit set was markedly higher in 2003, after the wetter year. The high level of abortion in 2002 (63% of immature fruits) might have been a consequence of winter-spring drought, although poor pollination and excessive predation cannot be ruled out as contributing factors. Whatever the reason for poorer fruit set in 2002, overall fruit production did not differ between years, apparently because higher flower production in 2002 compensated for lower fruit set.

The floral biology of *F. splendens* reflects the influence of plant size at several points. As plants grow in size, they produce more inflorescences (Fig. 6), thus augmenting annual flower production (Figs. 1, 3). Larger plant size does not necessarily translate into higher fruit production, however; pollinators might become less efficient outcrossers as they move among the many inflorescences on a large plant, and large plants might experience higher levels of resource limitation than small plants. Interannual variation in number of flowers per branch exists but is not large; the main constraint on annual flower production is likely plant size, particularly the number and length of branches that are reproductively active.

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THE EFFECT OF SEASONALITY OF BURN ON SEED GERMINATION IN CHAPARRAL: THE ROLE OF SOIL MOISTURE

DANIELLE LE FER¹ AND V. THOMAS PARKER

San Francisco State University, Dept. of Biology, 1600 Holloway,
San Francisco, CA 94132

ABSTRACT

Fire represents an important recruitment phase for many chaparral species. Prescribed burns are often scheduled during winter or spring when soil moisture is high in order to minimize risks of uncontrolled fire. However, chaparral wildfires typically occur in the summer or fall when soil moisture is low. Changing the seasonality of burn affects pre-burn soil moisture, burn temperature and timing of germination. High soil moisture during winter or spring burns is hypothesized to lower germination rates of chaparral plants compared to fall burns. The purpose of this study was to evaluate the effects of prescribed spring burns on the germination of chaparral species in the Mendocino National Forest, California. We conducted two experiments to test for effects of moisture on seed germination. In the soil heating experiment, soil collected under chaparral was heated at several temperatures and soil moistures, and germinating seeds were counted. In the seed heat treatment experiment, seeds of 13 species were heated moist and dry to determine the moisture effect on heated seeds. Results indicate a differential response of seeds to heat and soil moisture. *Lotus humistratus*, *Daucus pusillus* and *Penstemon heterophyllus* were negatively affected by temperature in both moist and dry treatments. *Ceanothus cuneatus* and *Genista monspesullana* germination increased with temperature in both dry and moist treatments. Germination of six species (*Adenostoma fasciculatum*, *Camissonia contorta*, *Emmenanthe pendiflora*, *Epilobium ciliatum*, *Galium aparine* and *Malacothrix clevelandii*) decreased under moist heat treatments. These results suggest that spring burns may lead to decreased diversity of chaparral due to reduced seed survival and germination of certain species.

Key Words: seasonal burns, chaparral, soil moisture, temperature, seed germination, prescribed burns, seed bank.

Fire has become an important management tool, to recreate or maintain specific vegetation communities (oak savanna, grassland, southeastern pine forest, tall grass prairie, chaparral), to maintain species diversity and endangered or rare species, and to control invasive species (Zedler and Scheid 1988; Minnich 1989; Keeley 1991). Fire as a biological process consists of a complex set of components (timing, intensity, duration, interval between burns), and “fire adapted” vegetation is typically adapted to a specific set of ranges of these components. Shifting the timing of fire can substantially affect vegetation structure, vegetation composition and the soil seed bank of a site (Kauffman and Martin 1991). In chaparral, the previously dormant soil seed bank is an important post-fire recruitment source (Keeley 1987). A better understanding of the effect of seasonality of burn on species diversity and seed bank composition would improve the ability of land managers to incorporate fire into management plans.

Chaparral structure and composition is greatly influenced by fire (Moreno and Oechel 1991). Chaparral is an evergreen sclerophyllous shrub vegetation that dominates in moderately xeric sites of

California that are characterized by seasonal drought (Christensen and Muller 1975a). The combination of dense shrub cover, severe summer drought and the accumulation of “fuel” in chaparral lead to frequent fires, with frequencies of once every 40 to 60 years in southern California (Christensen and Muller 1975b). Fires represent an important recruitment phase for many chaparral species: Diversity and seedling numbers are highest in the first and second growing seasons after fire (Christensen and Muller 1975b). Recruitment may be affected by changes in the fire regime, such as fire exclusion or very frequent fires (Keeley 1995; Zedler 1995; Keeley 2002).

In chaparral, winter and spring prescribed burns change some components of the fire regime. In particular, changing the seasonality of the burn from the fall to the spring affects soil moisture, timing of regrowth, and fire intensity (Parker 1990). Since seed response to heat and soil moisture varies according to seed water absorption, the seasonality of burn and soil moisture content can greatly influence germination patterns.

Timing of burns also has the potential to change the invasion regime of post-fire alien species (Kauffman and Martin 1991). For example, burning in early summer, just as plants begin to flower, prevents seed production of yellow star-thistle (*Centaurea solstitialis* L. [Asteraceae]) in grasslands in

¹ Current address: U.S.F.W.S., San Francisco Bay National Wildlife Refuge, P.O.B. 524, Newark, CA 94560, email: Danielle.Lever@fws.gov.

California. However, late spring and fall burns increase diversity of native species and decrease abundance of alien species (Hastings and DiTomaso 1996). In some cases, fire may allow invasive species like *Cytisus scoparius* L. (Fabaceae) and *Carpobrotus edulis* (Aizoaceae) to increase in numbers (Zedler and Scheid 1988; D'Antonio et al. 1993; Agee 1996). Thus, management strategies involving fire must take into account the mix of individual species with different life histories and responses to fire and the phenological timing of burns (Parker 1990; Glitzenstein et al. 1995; Spier and Snyder 1998).

Previous studies have examined the effect of heat on the seed response of chaparral species (Keeley and Nitzberg 1984; Keeley et al. 1985), but few studies have examined the effect of changing the seasonality of burn and soil moisture on seed germination at the time of fire. Understanding the effect of soil moisture at the time of fire can help predict the effect of burns on responses of individual species and the resulting species composition of the chaparral.

An important step in managing vegetation with fire is to classify taxa into ecological response groups, keeping in mind that each species has unique life history characteristics (Parker 1990). Two functional groups can be distinguished within a seed bank: Species that do not require fire for germination (fire-independent), and species which are fire-stimulated either via heat, smoke chemistry or some other mechanism (Parker and Kelly 1989; Zammit and Zedler 1994). Fire-stimulated seeds are adapted to surviving the heat produced in a fire, and represent about 21% of the total seed bank in chaparral (Zammit and Zedler 1994). Fire-independent seeds comprise almost 2/3 of the total seed bank in mixed chaparral; these species can potentially recruit at any point in the fire cycle, including immediately after fire (Zammit and Zedler 1994). Seeds of obligate resprouters, geophytes, perennial grasses and many introduced annuals are non-dormant and fire-independent (Zammit and Zedler 1994).

In California chaparral, higher rates of seed germination occur following autumn fires than spring fires (Parker and Kelly 1989). In laboratory experiments, germination is negatively affected for many species heated under moist conditions typical of spring burns (Rogers et al. 1989). Seeds lacking hard seed coats have lower heat tolerance after they have absorbed moisture (Parker 1990). Spring and winter burns, typically of lower heat intensity, may have a negative impact on species with hard seed coats that require high temperatures to germinate (e.g., *Ceanothus*) (Parker 1990).

The goal of this study was to examine the impact on the seed bank of spring prescribed burns in California chaparral. Our objectives were to determine the effect of changes in soil moisture and temperature during spring burns on seed germination in

the chaparral vegetation of the Mendocino National Forest, California. In order to examine seed bank response to soil moisture and heat treatments, we conducted two experiments. In the first experiment, germination was measured in soil heated in the laboratory under several moisture conditions. In the second experiment, seeds of selected species were heated dry and after imbibing water to determine moisture effects on specific species. Heat treatments were selected to duplicate soil temperatures during a burn (70°C to 110°C). Soil moisture treatments included expected summer soil moistures (3% to 7%) and possible spring soil moistures (17–30%).

METHODS

We obtained soil and seeds from the east slope of the Coast Range Mountains, in previously burned chaparral, in the Mendocino National Forest, in northern Glenn County, near Highway 162, north-west of Elk Creek, California USA (122°7'W, 39°72'N). The vegetation consisted primarily of *Adenostoma fasciculatum* Hook. & Arn. (Rosaceae) and *Ceanothus cuneatus* var. *cuneatus* (Hook.) Nutt. (Rhamnaceae). Soil samples were collected from the upper 5 cm of soil under mixed *Ceanothus* and *Adenostoma* chaparral in August 1994. All seeds except *Genista monspessulana* (L.) L. Johnson (Fabaceae) were collected in the Mendocino National Forest in 1994 and 1995. *Genista* seeds were collected from Old Railroad Grade on Mount Tamalpais in Marin and were selected for this experiment because its seeds are known to imbibe less than 5% of their dry weight, and the species is an invasive in chaparral.

Soil Experiment

We moistened the soil, and placed it in ziplock bags for one week to ensure even moistening. We conducted four heat treatments (control [unheated], 90°C, 100°C, and 110°C) and five moisture treatments (3%, 15%, 22% and 30% of soil dry weight), with four replicates per treatment. The soil was heated for 10 minutes in an oven, using soil probe thermometers to measure soil temperature. Samples were stratified at 5°C to 8°C for two weeks then placed in the greenhouse and 50 ml of charate (as per Keeley 1987) was added to each flat (20 cm × 20 cm). We monitored germination every two weeks over the course of 120 days.

Seed Experiment

We examined the effect of temperature on dry and moistened seeds of thirteen species: *Adenostoma fasciculatum*, *Ceanothus cuneatus* var. *cuneatus*, *Penstemon heterophyllus* Lindley (Scrophulariaceae), *Camissonia contorta* (Douglas) Raven (Onagraceae), *Mentzelia dispersa* S. Watson (Loasaceae), *Galium aparine* L. (Rubiaceae), *Daucus pusillus* Michaux (Apiaceae), *Malacothrix cleve-*

TABLE 1. MEAN NUMBER OF SEEDLINGS PER FLAT IN RESPONSE TO HEAT AND MOISTURE TREATMENTS IN SOIL COLLECTED IN CHAPARRAL IN THE MENDOCINO NATIONAL FOREST, CALIFORNIA. Values are mean numbers of seedlings per flat (SD) for each species (n = 4). Results of Kruskal-Wallis test followed by multiple range analysis on ranks. AB (within a row) represents moisture effect (result of comparison among moisture treatments within a temperature treatment); ab (within a column) represents heat effect within a soil moisture treatment (results of comparison among heat treatments). Treatments with the same letter are not significantly different. * P < 0.05; ** P < 0.01.

| | # Seedlings per flat (SD) | | | | | Moisture effect | |
|---------------------------------|------------------------------|-----------------------------|-----------------------------|----------------------------|--|-----------------|----------------|
| | Soil moisture | | | | | P | χ ² |
| | 3% | 15% | 22% | 30% | | | |
| Control: no heat | | | | | | | |
| <i>Adenostoma fasciculatum</i> | 4.75 (1.89) | 3.25 (1.70) ^{a***} | 4.66 (0.58) ^{a***} | 4.75 (2.5) ^{a***} | | 0.32 | 3.47 |
| <i>Ceanothus cuneatus</i> | 0 | 0.75 (0.5) ^{b**} | 1.33 (2.33) ^c | 0.75 (0.96) ^{b**} | | 0.32 | 3.48 |
| <i>Eriodictyon californicum</i> | 0.5 (1.00) ^{b***} | 0.25 (0.5) | 0 ^{a***} | 2.5 (1) ^{a***} | | 0.12 | 5.8 |
| <i>Gnaphalium californicum</i> | 0.25 (0.5) | 0 | 0 | 0 | | 0.43 | 2.8 |
| <i>Isopyrum stipitatum</i> | 0.25 (0.5) | 0.25 (0.5) | 0 | 0 | | 0.6 | 1.9 |
| <i>Navarretia pubescens</i> | 0 | 0.25 (0.5) | 0 | 0 | | 0.43 | 2.8 |
| Unknown | 0.25 (0.5) | 0.5 (0.58) | 0 | 0.25 (0.5) | | — | — |
| <i>Verbasicum thapsus</i> | 0 | 0 | 0 | 0.25 (0.5) | | — | — |
| Total Density | 5.75 (3.30) ^{b***} | 6.25 (4.03) | 7.33 (2.31) | 8.5 (3.32) | | 0.68 | 1.5 |
| 90°C | | | | | | | |
| <i>Adenostoma fasciculatum</i> | 1.75 (0.96) ^A | 0 ^B | 0 ^b | 0 ^{B b} | | 0.002 | 14.7 |
| <i>Ceanothus cuneatus</i> | 0.75 (0.96) ^B | 5.75 (1.70) ^{A a} | 6.5 (2.6) ^{A a} | 5.5 (2.38) ^{A a} | | 0.04 | 8.3 |
| <i>Eriodictyon californicum</i> | 0.5 (1.0) ^b | 0.25 (0.5) | 0 | 0 ^b | | 0.54 | 2.2 |
| Total Density | 2.75 (1.71) ^b | 6 (2.16) | 6.5 (2.64) | 5.5 (2.38) | | 0.16 | 5.2 |
| 100°C | | | | | | | |
| <i>Adenostoma fasciculatum</i> | 4 (2.16) ^A | 0 ^{B b} | 0 ^{B b} | 0 ^{B b} | | 0.003 | 13.6 |
| <i>Ceanothus cuneatus</i> | 1 (1.41) | 2.5 (2.64) ^{a b} | 2.5 (1.29) ^{b c} | 4.5 (2.38) ^a | | 0.12 | 5.9 |
| <i>Eriodictyon californicum</i> | 29 (18.16) ^{A a} | 0 ^B | 0 ^{B b} | 0 ^{B b} | | 0.004 | 13.6 |
| <i>Gnaphalium californicum</i> | 0.25 (0.5) | 0 | 0 | 0 | | — | — |
| Total Density | 34.25 (19.96) ^{A a} | 2.5 (2.65) ^B | 2.5 (1.29) ^B | 4.5 (2.38) ^B | | 0.02 | 9.4 |
| 110°C | | | | | | | |
| <i>Adenostoma fasciculatum</i> | 5 (3.46) ^A | 0 ^{B b} | 0 ^{B b} | 0 ^{B b} | | 0.007 | 12.1 |
| <i>Camissonia contorta</i> | 0.25 (0.75) | 0 | 0 | 0 | | — | — |
| <i>Ceanothus cuneatus</i> | 1.75 (1.70) | 2.5 (1.91) | 5.25 (2.06) ^{a b} | 1.75 (1.71) ^{a b} | | 0.16 | 5.1 |
| <i>Eriodictyon californicum</i> | 26.75 (20.15) ^{A a} | 0 ^B | 0 ^{B b} | 0 ^{B b} | | 0.004 | 13.6 |
| Total Density | 33.75 (18.41) ^{A a} | 2.5 (1.91) ^B | 5.25 (2.06) ^B | 1.75 (1.71) ^B | | 0.02 | 10.3 |

TABLE 2. PERCENT WATER ABSORPTION ([MOIST WEIGHT – DRY WEIGHT]/DRY WEIGHT) FOR SEEDS SOAKED 8 HOURS IN DISTILLED WATER.

| Species | Percent water absorption |
|--------------------------------|--------------------------|
| <i>Adenostoma fasciculatum</i> | 49.7 |
| <i>Camissonia contorta</i> | 70.0 |
| <i>Ceanothus cuneatus</i> | 4.2 |
| <i>Daucus pusillus</i> | 43.0 |
| <i>Dicentra chrysantha</i> | 25.1 |
| <i>Emmenanthe pendiflora</i> | 46.7 |
| <i>Epilobium ciliatum</i> | 187.0 |
| <i>Galium aparine</i> | 65.5 |
| <i>Genista monspessullana</i> | 0.0 |
| <i>Lotus humistratus</i> | 81.0 |
| <i>Malacothrix clevelandii</i> | 86.1 |
| <i>Mentzelia dispersa</i> | 5.5 |
| <i>Penstemon heterophyllus</i> | 71.3 |

landii A. Gray (Asteraceae), *Dicentra chrysantha* (Hook. and Arn.) Walp. (Papaveraceae), *Epilobium ciliatum* ssp. *ciliatum* Raf. (Onagraceae), *Emmenanthe penduliflora* var. *penduliflora* Benth. (Hydrophyllaceae), *Lotus humistratus* E. Greene (Fabaceae) and *Genista monspessulana* (L.) L. Johnson (Fabaceae).

We completed two sets of seed heat treatments: a set with pre-soaked seeds (soaked in distilled water for eight hours prior to heating) and a set with dry seeds. Seeds were heated in glass tubes in an oil bath heater containing sand for 10 minutes at 70°C, 90°C and 110°C. Temperature probes measured the heat in the tubes. One control set was not heated. After heat treatment, we placed seeds in Petri plates (25 seeds per plate) between two layers of Whatman no. 1 filter paper, and applied a 5 ml aqueous solution of charate, prepared as per Keeley (1987), then stratified seeds in an incubator. Petri plates were examined weekly for germination for up to 14 weeks, and germinated seeds were counted and removed.

Seeds of different species were stratified at specific combinations of light and temperature to maximize germination (Keeley and Keeley 1987; V.T. Parker, unpublished data). The seeds of *Adenostoma*, *Ceanothus*, *Malacothrix*, *Dicentra*, *Emmenanthe*, *Daucus*, *Galium* and *Epilobium* were stratified in the dark at 5°C for 3 weeks, then for 4 weeks with 12 hours of light (20°C) and 12 hours of darkness (5°C). This cycle was repeated once in order to maximize germination rates. *Camissonia*, *Penstemon* and *Mentzelia* seeds were first stratified in the dark (5°C) for 3 weeks, then with 12 hours of light (20°C) and 12 hours of darkness (5°C) for 4 weeks. For the second cycle they were placed at 30°C (dark) for 1 week, then at a regime of 12 hours of light and 12 hours of dark for 2 weeks. *Genista* and *Lotus* were stratified for 4 weeks in the dark at 5°C, then at 10 hours light (20°C) and 14 hours dark (5°C) for 3 weeks.

Data Analysis

We used a Kruskal-Wallis analysis followed by a multiple range analysis on ranks to compare germination of soil burn treatments (SAS 2004). For each species, we compared percentage germination for heat and moisture treatments with a two-way Analysis of Variance after arc-sine transforming the data, followed by multiple pair-wise comparisons (Tukey) to determine differences between moisture treatments and between control and heat treatments (SAS 2004).

RESULTS

Soil Experiment

Germination in soil heated under dry conditions (i.e., 3% soil moisture) varied among species. At 3% soil moisture, *Eriodictyon* germination increased significantly with heat ($P < 0.01$) (Table 1). Total density reflected the high germination of *Eriodictyon* (Table 1). *Eriodictyon* germinated in small quantities in the control and 90°C treatments (0.5 per flat); its densities increased significantly and were very high at 100°C and 110°C, reaching a high of 29 seedlings/flat at 100°C ($P < 0.01$) (Table 1). In contrast, *Ceanothus* and *Adenostoma* germination did not increase with heat (Table 1). For *Gnaphalium californicum* DC. (Asteraceae), *Iso-pyrum stipitatum* A. Gray (Ranunculaceae), *Navaretia pubescens* (Benth.) Hook. and Arn. (Polemoniaceae), and *Verbascum thapsus* L. (Scrophulariaceae), germination was too low to examine statistically (Table 1).

Eriodictyon, *Adenostoma* and total germination were negatively affected by heat under moist conditions (i.e., 15%, 22% and 30% soil moisture) (Table 1). *Eriodictyon* germination was significantly lower under moist conditions at soil temperatures of 100°C and 110°C ($P \leq 0.01$) (Table 1). *Adenostoma* germination decreased under moist conditions when the soil was heated ($P \leq 0.01$) (Table 1).

Total density decreased as temperature and soil moisture increased (Table 1). At low temperatures (no heat and 90°C), total density was not affected by soil moisture ($P > 0.05$) (Table 1). However, total density decreased significantly in moist soil at temperatures of 100°C and above ($P < 0.05$) (Table 1).

At 90°C, *Ceanothus* germination was higher under moist conditions (Table 1). At other temperatures, soil moisture did not affect *Ceanothus* germination. *Ceanothus* was the only species germinating in moist soil at temperatures above 90°C (Table 1).

Seed Experiment

Seed water absorption, as percent of dry weight ([moist weight – dry weight]/dry weight) ranged from 4% to more than 100% of their dry weight

TABLE 3. RESULTS OF TWO-WAY ANOVA FOLLOWED BY MULTIPLE PAIR-WISE COMPARISONS (TUKEY) TO DETERMINE THE EFFECT OF HEAT AND MOISTURE TREATMENTS ON PERCENTAGE GERMINATION OF SEEDS COLLECTED IN CHAPARRAL IN THE MENDOCINO NATIONAL FOREST, CALIFORNIA. Values are mean and standard deviation (SD) of percent germination. * indicates significant difference ($P < 0.05$) between heat treatment and control.

| Species | Heat treatment | | | | | | | | | | Heat effect |
|--|----------------|----|--------|----|--------|----|--------|----|--------|-------|-------------|
| | Control | | 70°C | | 90°C | | 110°C | | P | F | |
| | Mean | SD | Mean | SD | Mean | SD | Mean | SD | | | |
| <i>Adenostoma fasciculatum</i> (n = 8) | | | | | | | | | | | |
| Dry Treatment | 20 | 4 | 22 | 11 | 30 | 12 | 1 | 1 | <0.001 | 22.8 | |
| Moist Treatment | 19 | 9 | 2* | 4 | 0* | 0 | 0* | 0 | | | |
| P (dry vs moist) | | | <0.001 | | <0.001 | | | | | | |
| <i>Camissonia contorta</i> (n = 4) | | | | | | | | | | | |
| Dry Treatment | 6 | 5 | 63* | 11 | 47* | 14 | 35* | 24 | 0.001 | 7.1 | |
| Moist Treatment | 9 | 3 | 2 | 4 | 0 | 0 | 0 | 0 | | | |
| P (dry vs moist) | | | <0.001 | | <0.001 | | 0.004 | | | | |
| <i>Ceanothus cuneatus</i> (n = 8) | | | | | | | | | | | |
| Dry Treatment | 0 | 0 | 3 | 4 | 9 | 5 | 25* | 17 | <0.001 | 16.0 | |
| Moist Treatment | 1 | 1 | 8 | 11 | 20* | 10 | 20* | 15 | | | |
| P (dry vs moist) | | | | | | | | | | | |
| <i>Daucus pusillulus</i> (n = 8) | | | | | | | | | | | |
| Dry Treatment | 35 | 15 | 6* | 7 | 1* | 2 | 0* | 0 | <0.001 | 85.1 | |
| Moist Treatment | 32 | 10 | 0.5* | 1 | 0* | 0 | 0* | 0 | | | |
| P (dry vs moist) | | | | | | | | | | | |
| <i>Dicentra chrysantha</i> (n = 4) | | | | | | | | | | | |
| Dry Treatment | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 7 | 0.13 | 2.1 | |
| Moist Treatment | 0 | 0 | 3 | 3 | 0 | 0 | 1 | 1 | | | |
| P (dry vs moist) | | | | | | | | | | | |
| <i>Emmenanthe penduliflora</i> (n = 8) | | | | | | | | | | | |
| Dry Treatment | 58 | 17 | 55 | 7 | 3* | 4 | 40 | 17 | <0.001 | 84.2 | |
| Moist Treatment | 65 | 17 | 1* | 1 | 1* | 1 | 0* | 0 | | | |
| P (dry vs moist) | | | <0.001 | | <0.001 | | <0.001 | | | | |
| <i>Epilobium ciliatum</i> (n = 8) | | | | | | | | | | | |
| Dry Treatment | 57 | 8 | 55 | 10 | 45 | 15 | 15* | 3 | <0.001 | 112.5 | |
| Moist Treatment | 53 | 17 | 5* | 1 | 1* | 2 | 0* | 0 | | | |
| P (dry vs moist) | | | <0.001 | | <0.001 | | | | | | |
| <i>Galium aparine</i> (n = 8) | | | | | | | | | | | |
| Dry Treatment | 58 | 11 | 52 | 13 | 25* | 11 | 3* | 4 | <0.001 | 131.5 | |
| Moist Treatment | 61 | 13 | 0* | 0 | 0* | 0 | 0* | 0 | | | |
| P (dry vs moist) | | | <0.001 | | <0.001 | | | | | | |

(Table 2). *Ceanothus*, *Genista*, and *Mentzelia* seeds imbibed 4% or less of their dry weight in water. All other seeds absorbed 23% or more of their dry weight.

Three species (*Ceanothus*, *Genista* and *Camissonia*) showed a positive temperature effect on germination when heated dry (Table 3). *Ceanothus* germination increased from 0 at the control temperature to 25% at 110°C. *Genista* germination increased from 15% at no heat to 23% when heated. Germination of *Camissonia* seeds increased from 6% when unheated to as much as 63%.

In eight species, *Adenostoma*, *Emmenanthe*, *Epilobium*, *Galium*, *Daucus*, *Lotus*, *Malacothrix* and *Penstemon*, at least one heat treatment under dry conditions negatively affected germination (Table 3). Heat tolerance of species varied, but germination of all of the former species except *Emmenanthe* dropped at 110°C. *Daucus* and *Penstemon* were most sensitive to heat: germination dropped at 70°C. *Emmenanthe*, *Galium* and *Lotus* germination dropped at temperatures of 90°C. *Epilobium* was most tolerant of heat: germination dropped significantly at 110°C.

Germination of five species (*Ceanothus*, *Genista*, *Lotus*, *Daucus* and *Penstemon*) was not affected by moisture (Table 3). *Lotus*, *Daucus* and *Penstemon* seeds were negatively affected by temperature in both moist and dry treatments (Table 3). *Ceanothus* and *Genista* germination was higher when seeds were heated in both moist and dry treatments (Table 3).

Germination of six species (*Adenostoma*, *Camissonia*, *Emmenanthe*, *Epilobium*, *Galium*, *Malacothrix*) decreased under moist heat treatments at temperatures as low as 70°C (Table 3).

DISCUSSION

Levels of heat tolerance vary among species (Keeley et al. 1985; Keeley 1987; Keeley and Keeley 1987; Odion and Davis 2000), and high temperatures (150°C) can be lethal for seeds (Keeley et al. 1985; Cruz et al. 2003). For several fire-stimulated species in this study, germination decreased at 120°C.

The heat-stimulated seed germination (heat or chemical cues) observed in many species in this study (*Ceanothus*, *Camissonia*, *Lotus*, *Genista*, *Emmenanthe*) supports findings in other field and laboratory studies (Keeley and Nitzberg 1984; Keeley et al. 1985; Keeley and Keeley 1987; Moreno and Oechel 1991; Ferrandis et al. 1999). Also, *Adenostoma* has previously been observed to be sensitive to heat during winter burns (Moreno and Oechel 1991).

Soil moistures of 15%, equivalent to those occurring during spring burns in the Mendocino National Forest, had a negative impact on seeds with no seed coat dormancy (Le Fer 1998). Seeds that were negatively impacted by heat under moist con-

ditions (*Adenostoma*, *Camissonia*, *Galium*, *Epilobium*, *Malacothrix*, *Emmenanthe*) had no seed coat dormancy and absorbed water above 23% of their weight. These included seeds of opportunistic "fire survivors" that do not require fire to germinate and may survive low intensity heat (e.g., *Adenostoma*, *Epilobium*, *Galium*). A group of fire-sensitive post-fire colonizers was sensitive to any amount of heat, moist or dry (*Emmenanthe*, *Daucus*).

Conditions during spring prescribed burns may be conducive to germination of fire-stimulated seeds with seed coat dormancy (e.g., *Ceanothus*, *Genista*). Hard-coated seeds absorbed 4% or less of their weight in water and did not exhibit a negative temperature effect under moist conditions. *Ceanothus*, an obligate seeding shrub, may increase in numbers after spring burns. However, some spring burns may not reach temperatures high enough to stimulate *Ceanothus* seed germination (Parker 1989). Assuming seed longevity of about 50 years, any ungerminated seeds might die before the next fire (Parker 1989; O'Neil 2002), leading to decreased seed bank diversity. *Ceanothus* reaches sexual maturity at 20 years of age, at which time seed banks reach their highest levels (Zamitt and Zedler 1994). Ungerminated seeds are also susceptible to predation (Mills and Kummerow 1989; O'Neil 2002).

Seeds of shrub species that would germinate under the low moisture conditions typical of fall burns (e.g., *Eriodictyon* and *Adenostoma*), are negatively affected under conditions found during spring burns. *Adenostoma* may continue to dominate post-fire vegetation by resprouting. However, without the establishment of younger plants by germination, shrub density will eventually decline.

Diversity in the chaparral community is retained primarily within the seed bank (Sampson 1944; Sweeney 1956; Keeley and Keeley 1987; Parker and Kelly 1989). Spring prescribed burns may change the composition of the seed bank over time by differentially promoting germination of species with hard-coated seeds over those with soft-coated seeds. High soil moistures during burns negatively affect germination for many species that would survive fall burns, and this would likely lead to shifts in community composition. The impact of winter or spring burns may be particularly severe for fire-dependent herbaceous annuals with soft seed coats (e.g., *Emmenanthe*, *Epilobium*), since their seeds wouldn't survive fires under wet conditions, and may be depleted from the seed bank.

Fire can promote invasion of nonnative species (Zedler and Scheid 1988; D'Antonio et al. 1993). A late spring fire leads to germination the following spring, leaving an opportunity for nonnative species to disperse to and establish at the site (Parker 1989). The reduction in density and species richness of plants germinating from dormant seed banks also can give nonnative species an opportunity to become established (Parker 1989). Seeds of

some nonnative species (e.g., *Genista*) may germinate at high rates after spring fires, leading to increased eradication difficulties. The European invasive *Genista* can resprout after fire, and produces a large and persistent seed bank (Parker and Kersnar 1989), stimulated by moderate heat either from fire or summer heat (Parker 1993; Ferrandis et al. 1999).

Burns are an important component of chaparral management and many species require fire to germinate. However, shifting the fire regime to the winter or spring affects soil moisture, fire intensity and timing of germination. Burning during the dry season maintains historical fire regimes and thus decreases these alterations to the ecosystem's dynamics. If this is not feasible, selecting prescribed burn windows that minimize soil moisture may decrease negative impacts. In addition, post-fire monitoring of regeneration and community composition can provide information that increases our understanding of the effects of environmental variables (e.g., moisture, heat, time of year) on specific species.

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SEED GERMINATION OF SIERRA NEVADA POSTFIRE CHAPARRAL SPECIES

JON E. KEELEY^{1,2}, THOMAS W. MCGINNIS¹, AND KIM A. BOLLENS¹

¹ U.S. Geological Survey, Western Ecological Research Center, Sequoia National
Park, Three Rivers, CA 93271, USA

jon.keeley@usgs.gov

² Department of Ecology and Evolutionary Biology, University of California,
Los Angeles, CA 90095 USA

ABSTRACT

The California chaparral community has a rich flora of species with different mechanisms for cuing germination to postfire conditions. Here we report further germination experiments that elucidate the response of several widespread shrub species whose germination response was not clear and include other species from the Sierra Nevada, which have not previously been included in germination studies. The shrubs *Adenostoma fasciculatum* and *Eriodictyon crassifolium* and the postfire annual *Mentzelia dispersa* exhibited highly significant germination in response to smoke treatments, with some enhanced germination in response to heating as well. The shrubs *Fremontodendron californicum* and *Malacothamnus fremontii* were stimulated only by heat-shock treatments. Seeds buried in the soil for one year exhibited substantially higher germination for controls and most treatments. In the case of two postfire annuals, *Mimulus bolanderi* and *M. gracilipes*, germination of fresh seed was significantly greater with smoke or heating but after soil storage, over two-thirds of the control seeds germinated and treatment effects were not significant. These two annuals are generally restricted to postfire conditions and it is suggested that control germination of soil-stored seed may be a light-response (which was not tested here) as previously reported for another chaparral species in that genus.

Key Words: chaparral, fire, germination, heat-shock, seed dormancy, smoke.

Wildfires are a natural feature of California landscapes and many plant communities are composed of species that are well adapted to such periodic disturbances. The most widespread vegetation type in the state is chaparral and its postfire response has been well studied (Keeley 2000). Regeneration is from residual species present prior to the fire and colonization plays a relatively minor role in the postfire recovery. Resprouts from stems or roots and seedling recruitment from seed banks are the primary means of regeneration. A substantial number of species of both herbaceous and woody life forms produce dormant seeds that accumulate in soil seed banks (Parker and Kelly 1989).

Fire-triggered germination is the result of either heat-shock or chemical products of combustion, and species appear to utilize one or the other of these modes. Heat-shock stimulated germination is widespread in the Fabaceae, Rhamnaceae, Convolvulaceae, Malvaceae, Cistaceae, and Sterculiaceae, and is found in many ecosystems (Keeley and Fotheringham 2000). While an exhaustive study of germination characteristics for these taxa is lacking, those that use this strategy are described as “hard seeded,” with a prominent waxy cuticle and a dense palisade layer of sclerids that enforces dormancy by forming a water-impermeable barrier. Brief heat-shock above 75°C is generally sufficient to induce imbibition by loosening cells in selected parts of the seed coat. This is sufficient to overcome

dormancy in many species, although in some, heat-shock must be coupled with light and/or cold stratification (Keeley 1987).

For a substantial number of species with fire-triggered germination, heat-shock has no effect on germination, rather germination is induced by chemicals from combustion products (Keeley 1991). Charred wood was first shown to stimulate germination in the postfire annual *Emmenanthe penduliflora* (Wicklow 1977) and later reported for many other chaparral species (Keeley 1991). Smoke also stimulates germination of this species and can trigger germination directly and indirectly by binding to soil particles, followed either aqueous or atmospheric transfer to seeds (Keeley and Fotheringham 1997). Some chaparral species have complex germination behavior that couples smoke cues with other environmental cues such as cold stratification. One of the more interesting characteristics is that reported for *Dicentra chrysantha*, *Dendromecon rigida* and *Trichostema lanatum*, where seed dormancy could only be broken by a combination of long term soil burial followed by smoke (Keeley and Fotheringham 1998). Smoke also has been reported from species indigenous to mediterranean-climate shrublands in Australia (Roche et al. 1997) and South Africa (Brown 1993). One interesting observation made by researchers in the latter country is that commercial food flavoring known as “liquid smoke” is equally effective in triggering

germination of many smoke stimulated species (Jager et al. 1996).

The bulk of the studies in California chaparral have focused on southern California species and very little attention has been directed at other parts of the state. In addition, the vast majority of work has been directed at annual species and less attention has been given to the germination behavior of the dominant shrub species. For example, the nearly ubiquitous *Adenostoma fasciculatum* (chamise) has never been tested for its response to smoke and prior studies have reported seemingly conflicting responses. For example, Stone and Juhren (1953) reported that heat alone would stimulate germination of *A. fasciculatum*, however, others have reported that heat does not stimulate germination but charred wood does (Parker 1987; Keeley 1987). Similar conflicting reports are noted for other woody species such as *Fremontodendron californicum* (Keeley 1991).

The purpose of the present study was to examine germination behavior of woody and herbaceous species from recently burned chaparral in the Sierra Nevada foothills. Postfire response of chaparral in this region has received relatively minimal study (Stocking 1966; Parsons 1976; Rundel et al. 1987; Rice 1993) and very little on natural fire-type cues for germination. Stocking (1966) reported that several Sierra Nevada fire following species such as the shrub *Malacothamnus fremontii*, a central California endemic, were stimulated to germinate by seed coat scarification. However, both smoke-stimulated and heat-stimulated species respond to this artificial treatment (Keeley and Fotheringham 1998), so it is unknown what the natural germination cue is for this species. Similarly, Rogers (1949) reported that a Sierra Nevada manzanita, *Arctostaphylos viscida*, is stimulated to germinate by scarification but could not identify the fire cue. Our study focuses on eight species that recruit seedlings in first year burned sites in the Sierra Nevada. We chose species that are either endemic to the region and not previously studied or more widespread species for which we could not ascribe any clear germination response. We investigated the effect of a range of heat-shock treatments and liquid smoke treatments on fresh seeds and seeds buried outside in soil for approximately one year.

METHODS

Species and Experimental Design

Eight species were selected for study, five shrubs and three annuals. Seeds from the annuals were collected from recently burned sites in Fresno County and seeds of the shrubs were from mature chaparral in Fresno and Tulare counties. Nomenclature is according to Hickman (1993). Seeds were cleaned of fruit material and other debris and stored dry in paper bags at room temperature for approximately 6 months, or in nylon mesh bags in soil outdoors

in Three Rivers, Tulare County, California (520 m elevation) for approximately one year.

Understanding germination response to fire cues such as smoke or heat-shock is complicated by the fact that the same factors that stimulate germination at particular levels are lethal at higher levels. Levels stimulatory to some species may be lethal to other species and levels stimulatory to some species may be insufficient to trigger germination in other species (Keeley and Fotheringham 1998). As a consequence, correctly interpreting negative responses requires a response curve that includes a range of levels from low to high for both smoke and heat.

For our smoke treatment we used a commercial liquid smoke (Wright's Concentrated Hickory Seasoning, B&G Foods, Inc.) diluted with distilled water. This product comes in a highly concentrated form and preliminary trials suggested the appropriate range to use was dilutions of 1:100, 1:500 and 1:1000. Heat-shock treatments included 80°C for 1 hr, and 5 min at 100°C, 110°C, 130°C, 140°C and 150°C. The three highest heating treatments were not done on soil-stored seeds due to limited seed availability. Thus, there were a total of 9 treatments and a control. Each treatment was replicated three times. Replicates comprised 30 seeds each for all species except for those with much larger seeds and smaller seed collections; $n = 15$ for *Arctostaphylos viscida* and *Malacothamnus fremontii* and $n = 10$ for *Fremontodendron californicum*.

Germination Experiments

Seeds to be heat-treated were placed in 70 × 15 mm aluminum dishes and treated in a forced convection oven. For the brief heat treatments, there was substantial spatial variation in temperature in different parts of the oven, although this was not a complication for the 1 hour treatment. Trials using thermocouples indicated that between the front and the back of the oven temperatures might have varied as much as $\pm 5^\circ\text{C}$ at low temperatures and as much as $\pm 10^\circ\text{C}$ at the highest temperature. In addition there was temporal variation due to the drop in temperature when dishes at room temperature were placed inside. To reduce this variation, multiple batches of replicates were treated separately. Nonetheless, temperatures reported here are the average temperature in the middle of the oven and only approximate the temperature any given replicate was exposed to. They are not meant to clearly define temperature optima but rather evaluate whether or not there is a germination response to heat-shock *per se*.

Germination was conducted in 60 × 15 mm sterilized polystyrene petri dishes with two pieces of 55 mm Whatman No. 1 filter paper and germination was initiated with the addition of 1.5–2.0 ml of distilled water, depending on the size of the seeds, for controls and heat-treated treatments or with a similar quantity of liquid smoke dilutions. Petri dishes

TABLE 1. ANALYSIS OF VARIANCE FOR GERMINATION EXPERIMENTS WITH FRESH LAB-STORED AND ONE YEAR SOIL-STORED SEEDS.

| Species | Fresh lab stored seed | | | One year soil-stored seed | | |
|-------------------------------------|-----------------------|---------------------|-----------------|---------------------------|---------------------|-----------------|
| | df | <i>F</i> -statistic | <i>P</i> -value | df | <i>F</i> -statistic | <i>P</i> -value |
| <i>Adenostoma fasciculatum</i> | | | | | | |
| Treatment | 9 | 9.748 | <0.001 | 6 | 6.749 | <0.01 |
| Error | 20 | | | 14 | | |
| <i>Arctostaphylos viscida</i> | | | | | | |
| Treatment | 9 | 1.976 | >0.05 | 6 | 1.129 | >0.05 |
| Error | 20 | | | 14 | | |
| <i>Eriodictyon crassifolium</i> | | | | | | |
| Treatment | 9 | 7.648 | <0.001 | 6 | 19.550 | <0.001 |
| Error | 20 | | | 14 | | |
| <i>Fremontodendron californicum</i> | | | | | | |
| Treatment | 9 | 13.094 | <0.001 | 6 | 20.878 | <0.001 |
| Error | 20 | | | 14 | | |
| <i>Malacothamnus fremontii</i> | | | | | | |
| Treatment | 9 | 14.870 | <0.001 | 6 | 63.834 | <0.001 |
| Error | 20 | | | 14 | | |
| <i>Mentzelia dispersa</i> | | | | | | |
| Treatment | 9 | 14.178 | <0.001 | 6 | 62.236 | <0.001 |
| Error | 20 | | | 14 | | |
| <i>Mimulus bolanderi</i> | | | | | | |
| Treatment | 9 | 2.881 | <0.05 | 6 | 9.749 | <0.001 |
| Error | 20 | | | 14 | | |
| <i>Mimulus gracilipes</i> | | | | | | |
| Treatment | 9 | 8.568 | <0.001 | 6 | 5.644 | <0.01 |
| Error | 20 | | | 14 | | |

were placed in a single layer on plastic trays and enclosed in heavy plastic zip-lock bags to reduce evaporation and transfer of gases between treatments. Trays were stored for 1 month under variable light conditions at ~4°C, followed by incubation at alternating 12 h in the light at 18°C and 12 h in the dark at 12°C. Seeds were examined weekly for at least 6 weeks and germinated seeds recorded and removed. Germination was determined as the emergence of the epicotyl, and for the smaller seeds, was done under a 7× dissecting scope, once a week for one month.

A subsample of seeds was cut and if seeds were hollow or shrunken they were considered inviable. This was considered an upper estimate of viability as no further tests were performed. Final germination was expressed as a percentage of apparently viable seeds. Percentage germination was arcsin transformed prior to analysis. Treatments were analyzed with one-way ANOVA. Pairwise comparisons were made with the Bonferroni post hoc test. For a few cases in which treatments indicated increased germination, but it was not statistically significant, a power analysis was performed to determine the necessary sample size required to obtain a significant difference ($P < 0.05$) from controls. For these analyses the average observed standard

deviation for controls and treatments was used. All analysis and graphics were run with SYSTAT 10.2 (www.systat.com).

RESULTS

Freshly collected seeds exhibited significant treatment effects with the exception of *Arctostaphylos viscida* (Table 1). Although most species exhibited some increased germination in response to both smoke and heat-shock, only one or the other was significantly different than controls (Fig. 1). Two shrubs, *Adenostoma fasciculatum* and *Eriodictyon crassifolium*, and two herbs, *Mentzelia dispersa* and *Mimulus bolanderi*, exhibited significantly greater germination for one or more of the smoke treatments over controls, but not for any of the heating treatments. Two shrubs, *Fremontodendron californicum* and *Malacothamnus fremontii*, and one herb, *Mimulus gracilipes*, had significantly greater germination for one or more of the heating treatments, but not for any of the smoke treatments. *Arctostaphylos viscida* germination did increase with smoke treatment but with the sample size of $n = 3$ it was not significant. Power analysis indicated that with the variance observed in these data

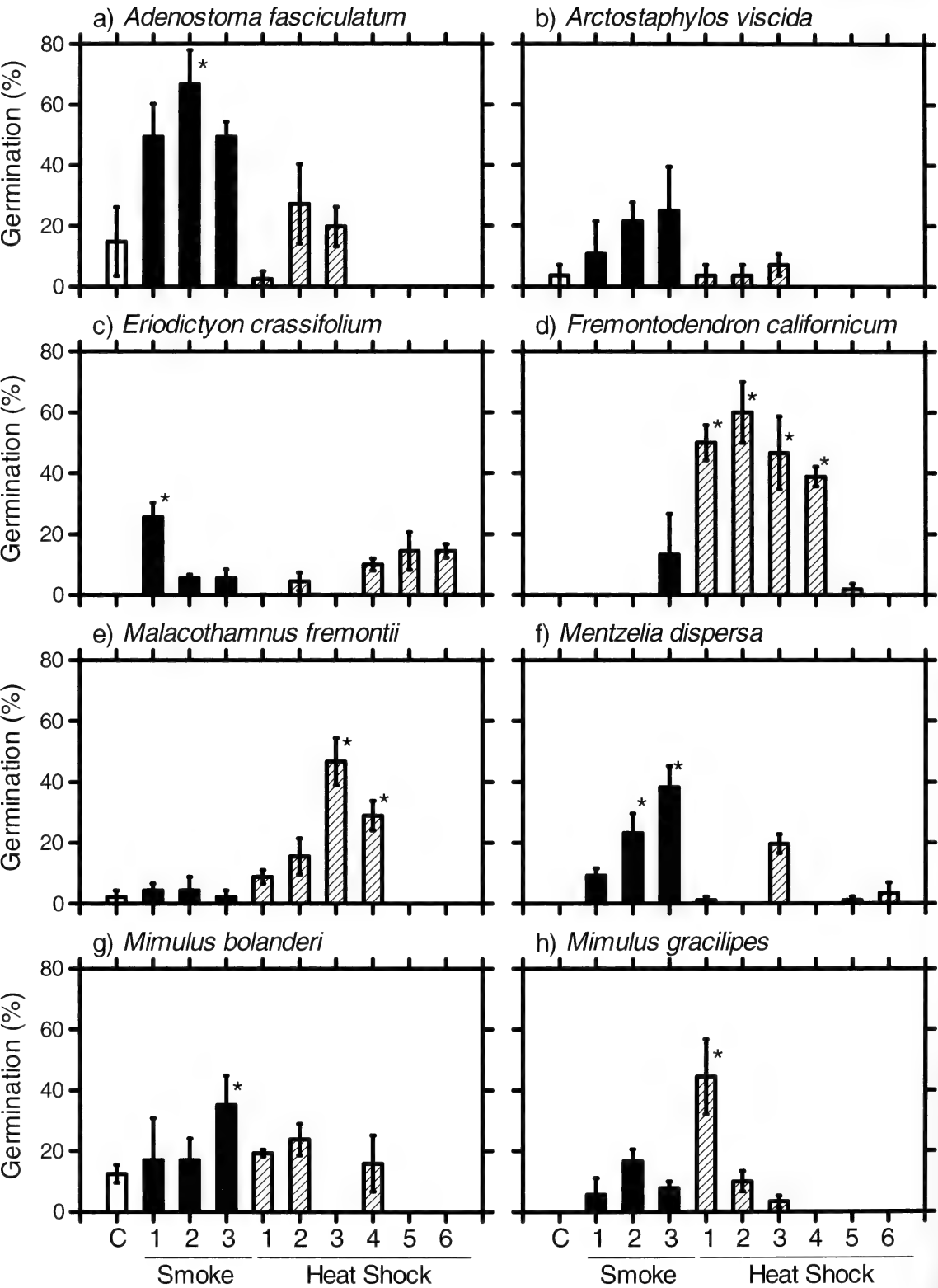


FIG. 1. Germination of freshly collected lab-stored seed of Sierra Nevada chaparral species in response liquid smoke (closed bars) at dilutions of 1 = 1:100, 2 = 1:500, 3 = 1:1000 and heat-shock (hashed bars) of 1 = 80°C for 1 hr, 2 = 100°C for 5 min, 3 = 110°C for 5 min, 4 = 130°C for 5 min, 5 = 140°C for 5 min, and 6 = 150°C for 5 min. Treatments significantly less than controls (open bars) at P < 0.05 are indicated with a *.

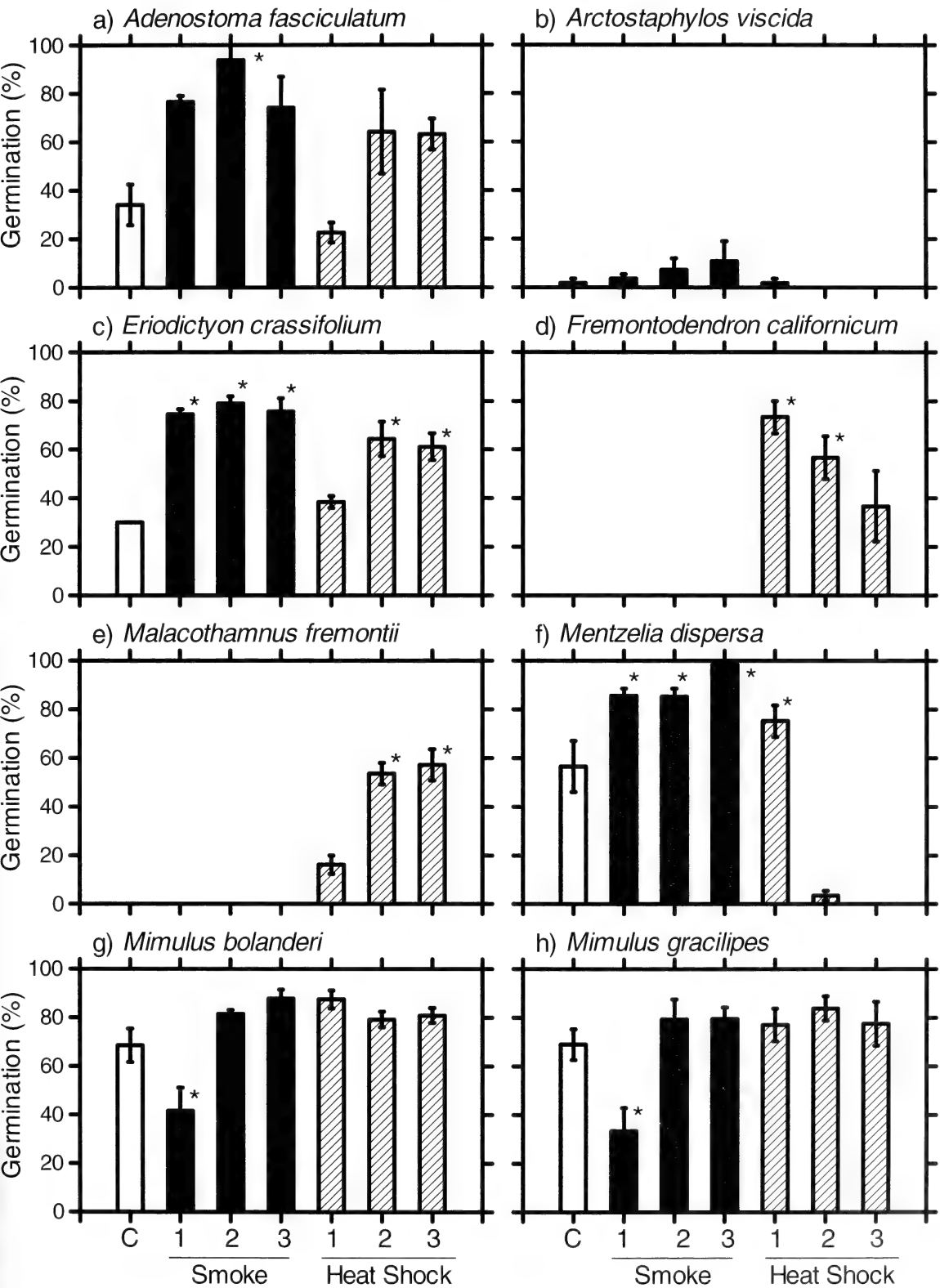


FIG. 2. Germination of seeds stored in outdoors in soil for approximately 1 year; in response to liquid smoke (closed bars) at dilutions of 1 = 1:100, 2 = 1:500, 3 = 1:1000 and heat-shock (hatched bars) of 1 = 80°C for 1 hr, 2 = 100°C for 5 min, and 3 = 110°C for 5 min (higher heating treatments not done on these seeds). Treatments significantly less than controls (open bars) at $P < 0.05$ are indicated with a *.

that it would require a sample size of $n = 68$ to detect a difference at the $P < 0.05$ level.

Germination of soil-stored seeds was greater for all species, with the exception of *Arctostaphylos viscida* (Fig. 2). In most cases, control germination was significantly greater than in freshly collected seeds. Responses to treatments were generally unchanged with a few differences. In *Adenostoma fasciculatum*, smoke was the only treatment that resulted in significantly greater germination than controls. Heating treatments did not increase germination significantly and power analysis indicated a sample size of $n = 40$ would be required to demonstrate a significant effect at the $P < 0.05$ level. In the case of *Eriodictyon crassifolium* and *Mentzelia dispersa*, germination was significantly increased by both smoke and heating, whereas with freshly collected seed it was only significant with smoke. For both *Mimulus* species control germination was over 60% and the only significant effect was reduced germination for the highest smoke concentration. However, both smoke and heat-shock did increase germination and power analysis indicated that with a sample size of $n = 40$ this would be significant at the $P < 0.05$ level.

DISCUSSION

For the chaparral species studied here seedling recruitment is largely restricted to the first postfire growing season. Colonization plays a minor role and the vast majority of recruitment arises from dormant soil-stored seed banks (Keeley 2000). Although seed banks have not been investigated for most of these species, we can infer their existence because they do not have propagules designed for long distance dispersal, and the time between fires and the first growing season is outside the season of seed dispersal. Our germination experiments indicate fire is a potential trigger for germination of the dormant seed bank and that these species in Sierra Nevada chaparral respond to either heat-shock or smoke.

This study clarifies the germination response of the widespread *Adenostoma fasciculatum*, which had not previously been clearly elucidated; heat-triggered germination (Stone and Juhren 1953) and other reports indicated chemical products of combustion in charred wood stimulated germination (Parker 1987; Keeley 1987). Here we found smoke to significantly increase germination, and in all likelihood the stimulatory chemicals are the same as in charred wood (Keeley and Fotheringham 2000). Heat may also increase germination but power analysis indicated that we would need much larger sample sizes to demonstrate a significant effect, thus heat-shock is perhaps a minor factor in the fire-stimulated germination response or it responds to a specific temperature range and duration not tested here.

The Sierrean *Arctostaphylos viscida* germination

is triggered by smoke and is similar to other species in the genus, which also have been reported to respond to combustion products such as charred wood (Keeley 1991). The very low germination is also quite similar to that reported for other species in the genus and suggests that either our crude estimate of viability was way off or there are other factors that are necessary to trigger germination of the entire seed bank.

For heat-stimulated species, significantly greater germination was observed when heated for 5 min between 100–130°C. For all species, heat-shock treatments of 5 min duration 140°C and above were apparently lethal.

These studies also provide further examples of changes in germination behavior following long term soil storage. Previous studies have shown that for several chaparral species a combination of soil burial followed by smoke treatment could overcome dormancy in deeply dormant seed banks, although burial alone could not (Keeley and Fotheringham 1998). The present study shows that soil storage generally increased germination of controls and treatments for most species. One interesting effect was the greatly increased control germination of *Mimulus* species following soil burial and the increased sensitivity to concentrated smoke solutions (Fig. 2). The fact that two-thirds of the control seeds germinated after soil burial seems to be at odds with the natural history of these two postfire annual species that are largely restricted to recently burned sites. One clue to what might explain this apparent discrepancy is the report of light-dependent dark-imposed dormancy for the chaparral species *Mimulus aurantiacus*, which can be overcome by smoke. In the light, this species germinates readily without smoke, but in the dark its germination is triggered by smoke.

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FACTORS CONTRIBUTING TO THE SOIL SEED BANK SIZE OF TWO OBLIGATE SEEDING *CEANOTHUS* SPECIES IN NORTHERN CALIFORNIA

SUSAN E. O'NEIL¹ AND V. THOMAS PARKER

Department of Biology, San Francisco State University, 1600 Holloway Avenue,
San Francisco, CA 94132

ABSTRACT

In fire-prone vegetation, non-sprouting, obligate-seeding species depend on a persistent seed bank to reestablish post-fire populations. Thus, for such seeds, seed development and survival in the soil are critical life history stages. The objectives of our study were to examine the structure and composition of *Ceanothus* seed banks, analyze the viability of seeds in the soil, and determine rates of predation before and after seed dispersal. This study focused on populations of *Ceanothus jepsonii* var. *albiflorus* (J. Howell), which is restricted to serpentine soils. We also included data on *Ceanothus cuneatus* (Hook.) Nutt., a widespread, non-restricted species, for comparison. We found that the seed bank of *C. jepsonii* loses seeds due to destruction or removal at several stages of development. Pre-dispersal seed predators attacked 37% of inflorescences included in experimentation and up to 50% of shrubs from which fruits were collected, post-dispersal predators removed over 70% of seeds in the litter. There was a 30% reduction in viability of older intact *C. jepsonii* seeds in the soil compared to seeds collected from plants during the study. A beetle in the genus *Zabrotes*, not previously known to oviposit on *Ceanothus*, was determined to be a causal agent of pre-dispersal seed predation, with other pre-dispersal predators and parasites also possible. These findings suggest that *Ceanothus* seed banks are quite dynamic and subject to a variety of seed losses during several stages prior to germination, which may ultimately be responsible for soil seed banks remaining relatively constant rather than building up over time.

Key Words: chaparral, *Ceanothus*, obligate seeder, seed predation, soil seed bank.

In Mediterranean climates, plant species have developed a variety of mechanisms to cope with and thrive in fire-prone habitats. Some species are able to resprout from vegetative structures not destroyed in fires, such as burls (Keeley and Zedler 1978). Other species retain their seeds in aboveground serotinous structures that open from the heat of wild-fire, releasing seeds to re-establish the populations post-fire; this response is more common in *Banksia* and other southern hemisphere genera, but is also utilized by some *Cupressus* and *Pinus* species in the northern hemisphere (Ne'eman et al. 1999). Another coping mechanism involves producing a persistent soil seed bank that responds to wildfire after the adult plants have been destroyed. Referred to as obligate seeding (Wells 1969; Keeley and Zedler 1978), this fire response syndrome has evolved in many shrub genera in fire-prone habitats, such as *Arctostaphylos* and *Ceanothus*, in California chaparral. Both genera have species that resprout and species that are obligate seeders. This study will focus on two obligate seeding *Ceanothus* species in Northern California.

In obligate seeding species, adult plants do not have the ability to resprout and are almost always killed in a wildfire. While persistent soil seed banks vary considerably in size (Parker and Kelly 1989), species in both *Ceanothus* and *Arctostaphylos* do

not seem to accumulate a larger seed bank over time once reproductive maturity has been reached (Keeley 1977, 1987a; Zammit and Zedler 1988, 1994). *Ceanothus* species often have substantially smaller seed banks than other chaparral species with persistent soil seed banks, even with the copious flower and fruit production typical in *Ceanothus* species (Keeley 1977; Parker and Kelly 1989; Zammit and Zedler 1994). For obligate seeding species, factors influencing the seed bank may greatly influence the future of the population.

Seeds are vulnerable at different stages from embryo formation through germination (Cavers 1983; Fenner 1985). During development on the parent plant, seeds are subject to pre-dispersal seed predation. Once dispersed, the remaining seeds are then exposed to seed predators (Louda et al. 1990). For seeds that must survive for years in the soil, the length of time prior to germination extends their vulnerability. The longer a seed resides in the soil, the greater it's risk of losing viability, or of being eaten, attacked by fungi or pathogens, or removed from a safe site (Cavers 1983; Fenner 1985; Simpson et al. 1989).

Pre-dispersal seed predation typically involves insect adults or larvae eating a seed, effectively destroying it before dispersal from the parent plant. These reductions in seed production are variable, but seed loss from the potential seed bank exceeds 90% in some species (Fenner 1985; Auld and Myerscough 1986; Hegazy and Eesa 1991; Sallabanks and Courtney 1992; Sheppard et al. 1994).

¹ Current address: National Park Service, 1 Bear Valley Road, Point Reyes Station, CA 94956. Email: segoneil@yahoo.com

While researchers have noted pre-dispersal seed predation as an important factor in seed bank dynamics in chaparral, few have actually documented it (Zammit and Zedler 1993; Boyd 2003). Previous studies have noted pre-dispersal seed predation on *Ceanothus sanguineus* in Idaho caused by a seed wasp (*Eurytoma squamosa*), a seed weevil (*Phyllotrox rutilis*), and a caterpillar (probably Gelechiidae) (Furniss et al. 1978). Huffman (2002) found seed predation by the same seed wasp, *Eurytoma squamosa*, on the resprouting *Ceanothus fendleri* in Arizona.

Once a seed is dispersed from the parent plant, it faces a high probability of predation while in the soil seed bank. Experiments on seed predation in chaparral suggest that vertebrates and invertebrates significantly reduce the size and modify the composition of soil seed banks (Keeley and Hays 1976; Evans et al. 1987; Mills and Kummerow 1989; Keeley and Parker 1990; Borchert et al. 2003). *Ceanothus* seeds are larger in size than most other chaparral species; therefore, they may be more attractive to predators such as rodents, birds and harvester ants (Price 1983; Mills and Kummerow 1989; Hoffmann et al. 1995). In a study by Smith (1942), *Ceanothus* seeds were found in the stomach contents of a large number of brush field pocket mice (*Perognathus parvus mollipilosus*).

Ceanothus jepsonii E. Greene (Rhamnaceae) is an obligate seeding species in the subgenus *Cerastes* and is restricted to serpentine soils. There are two varieties, both endemic to northern California. The range of *Ceanothus jepsonii* var. *jepsonii* includes Marin, Sonoma and western portions of Lake and Napa Counties. *Ceanothus jepsonii* var. *albiflorus* J. Howell (hereafter *C. jepsonii*) is found in eastern Lake, Napa, Yolo and Solano Counties and is the focal taxon of this study. Plants are erect, evergreen shrubs that are typically 1 m tall at the study site. Flowering typically begins in April and mature seeds are explosively dispersed in July–August. The seed rain of *Ceanothus* extends from under the canopy to a maximum distance of 9 m from the parent shrub (Evans et al. 1987), but seeds are most often found 1–3 m from the parent plant (Parker and Kelly 1989). The average seed size is 3–4 mm. The species is not currently considered threatened or endangered, but future conservation may be of concern because it is restricted to a specific habitat and soil type, which is undergoing development as people move into the wildland urban interface.

For comparison, we include data on *Ceanothus cuneatus*, an obligate seeding species also in the subgenus *Cerastes*. It is not restricted by soil type and has a wide range from Oregon to Baja California. Phenology and seed rain are similar to that of *C. jepsonii* (Evans et al. 1987). Mature *C. cuneatus* shrubs can be up to twice the height of *C. jepsonii* at the study site. The seeds of *C. cuneatus* are typically 25% smaller than those of *C. jepsonii*.

Species in the subgenus *Cerastes* may live up to 100 years (Keeley 1975), and are dominant shrubs in the mature chaparral stands that were used for experimentation.

The focal objective of our study was to examine the structure and composition of *Ceanothus* seed banks, using a restricted and a non-restricted species. Based on our findings, we: 1) Analyzed the viability and location of seeds in the soil seed bank; 2) Determined the impact, timing, selectivity and causal agent(s) of pre-dispersal seed predation; and 3) Examined the rates of post-dispersal seed predation in *C. jepsonii* seed banks.

METHODS

Study Site

The study was conducted at the Donald and Sylvia McLaughlin University of California Natural Reserve (McLaughlin Reserve hereafter; lat. 38°51'N, long. 122°24'W). The reserve covers 2,800 ha encompassing parts of Napa, Yolo and Lake Counties in the inner north coast range of California (see Harrison et al. 2003 and Safford and Harrison 2004 for a more detailed description of the site). We selected two primary serpentine sites at the reserve for experimentation, both west-facing with similar slopes: Research Hill and Site B. These study sites were not burned by a 1999 arson fire on the reserve (Safford and Harrison 2004). According to California Department of Forestry and Fire Protection, a significant fire has not occurred on the study sites since at least 1950 when they started recording and mapping fires in the state (www.frap.cdf.ca.gov). Additionally, local residents estimate that the last fire at the experimental sites was over 30 years ago (pers. comm. Scott Moore, McLaughlin Reserve Manager).

A secondary serpentine site, along Butts Canyon Road in Napa County, California was selected for supplemental data collection. This site was chosen primarily due to accessibility and distance from the primary experimental sites (approximately 48 km from the McLaughlin Reserve). A site on the northern border of the McLaughlin Reserve was selected for non-serpentine *C. cuneatus* experimentation with an additional non-serpentine seed collection site along Morgan Valley Road in Lake County, California. Attributes other than soil type and approximate stand age were not considered in secondary site selection.

Seed Bank Structure

To determine the depth of seeds in the soil column, we collected soil beneath a total of 31 *C. jepsonii* shrubs in the fall of 2000: 7 at Research Hill, 14 at Site B, and 10 along Butts Canyon Road. At each collection site, a 20-cm by 20-cm frame was placed directly under the outer canopy edge of each shrub. Soil and litter within the frame was collected

in 2-cm layers, and each layer was separated into individual bags. The layers represent 0–2 cm, 2–4 cm and 4–6 cm depths of the soil column. For samples with a litter layer, the litter layer was combined with the first (0–2 cm) layer of soil. At these sites, serpentine soils are markedly shallow and bedrock is often encountered at or before 6 cm in depth. Due to shallow soils, the sample size for the 4–6 cm layer under *C. jepsonii* is 25 rather than 31. Soil samples were dried in paper bags at room temperature.

We determined seed density in each soil layer through germination. Each sample was placed in a 20-cm \times 20-cm aluminum pan with small drainage holes and 1 cm of river sand on the bottom to help retain moisture (Zammit and Zedler 1994). Each sample was heated in an oven for 30 min at 100°C to stimulate germination by breaking the seed coat (Keeley 1987b; Bell et al. 1993; Garrett 2002). Thermocouples in the soil samples could not be monitored inside the oven, so 30-minute treatments were timed from when the oven, with the sample inside, reached 100°C. We made the assumption that seeds in the samples would reach a temperature sufficient to break the seed coat within that time period. The samples did not undergo a stratification treatment other than being housed in a non-heated greenhouse during the winter which was presumed to be enough of a stratification treatment to overcome dormancy (Odion and Davis 2000). Samples were watered and monitored daily from January through September of 2001. Each seedling that emerged was identified and clipped or repotted if identification was not possible in the seedling stage. Care was taken not to disturb the soil during transplanting.

Data for genera other than *Ceanothus* are not included in the present study. We used a repeated measures ANOVA to analyze soil column seed density. We report univariate *F*-tests with degrees of freedom adjusted using the Huynh-Feldt ϵ to correct for lack of sphericity of the variance covariance matrices (O'Brien and Kaiser 1985).

We repeated the same methods on 31 non-serpentine chaparral samples taken from the site at the reserve's northern boundary for comparison. Each sample was collected directly under the outer canopy edge of a *Ceanothus cuneatus* shrub. Samples were treated and data analyzed in the same manner as for *C. jepsonii*.

Seeds in the Soil

To determine the proportions of intact preyed upon and undeveloped seeds in the soil seed bank, we collected another series of soil samples underneath the canopy of nine *C. jepsonii* shrubs at Research Hill in the fall of 2000. The samples were collected using 20-cm \times 20-cm frames and were equal in volume (6 cm down soil column). The soil was brought back to the lab and dried at room tem-

perature. *Ceanothus jepsonii* seeds were removed by sifting with a series of soil sieves. Seeds were thoroughly inspected and categorized into intact, preyed upon (hollow with an exit hole), and undeveloped (typically deflated-looking and obviously inviable) (Hoffman et al. 1989; Zammit and Zedler 1993; Huffman 2002). These data were analyzed using a one-way ANOVA.

Seed Viability

To assess the viability of fresh intact seeds versus older intact seeds from the soil, two batches of *C. jepsonii* seeds were subjected to tetrazolium-chloride (TZ) testing. One batch included 192 fresh seeds collected directly from adult plants at Site B during 2001. A second batch consisted of 112 seeds collected during the previously mentioned seed type study. These seeds were intact and solid but showed signs of aging such as discolored or scratched seed coats. The TZ test is a method of assaying seed viability that can be done on dormant seeds (Moore 1962). If a seed has functioning mitochondria, the tissue will stain red (Freeland 1976). Respiring seeds were considered viable. The test was conducted by the Oregon State University Seed Laboratory following specifications normally used for hard-coated seeds.

Timing of Pre-dispersal Seed Predation

In the spring of 2001, we excluded insects from inflorescences starting at different times throughout the flowering season to assess the timing of pre-dispersal seed predation during seed development. Prior to the placement of exclosures, we hand-pollinated and flagged five inflorescences on a total of 30 shrubs at Research Hill and Site B. Hand pollination was done using fine paint brushes and transferring pollen from the flower of one shrub to the exposed style of a flower on another nearby shrub. The inflorescence branches were covered with 2-inch by 3-inch insect mesh sleeves to prevent insects from accessing the developing seeds at approximately two-week intervals starting at the onset of blooming through fruit maturation (Andersen 1988; Greig 1993).

The 30 shrubs chosen for experimentation were categorized phenologically into early- and late-blooming cohorts. The early-blooming cohort (10 shrubs at Research Hill and 10 shrubs at Site B) received their first treatment on March 30. The late-blooming cohort received their first treatment on April 11. The fifth and final exclosure treatment for all 30 plants was installed on June 22. Seeds covered during the final treatment were exposed to seed predators throughout development on the parent plant. All exclosures, acting as seed traps during dispersal, were collected on July 1. Fruits and seeds were brought back to the lab and the seeds of each inflorescence were dissected. If at least one seed per inflorescence had a larva inside, the inflores-

cence was considered attacked. In some cases, once an inflorescence was considered attacked, further seed dissection was halted and the remaining seeds were monitored for adult insect emergence for identification. Unfortunately, this precluded us from analyzing predation rates by seed rather than by inflorescence.

Host Specificity and Distribution of Pre-dispersal Seed Predator

After determining that pre-dispersal seed predator(s) were attacking *C. jepsonii* at Research Hill, we then set out to evaluate if the predation was occurring on *C. cuneatus* at the same site and if it occurs on both species in other locations. We collected fruits from 10 co-occurring *C. cuneatus* shrubs at Research Hill. We also collected fruits from 10 *C. jepsonii* shrubs from a serpentine chaparral site 48 km from Research Hill, and from 10 *C. cuneatus* shrubs growing on non-serpentine soil 7 km from Research Hill. All fruits were placed in direct sun for 10 hours to dry and explosively expel seeds from the capsule. Fruits that did not explode were cracked using pliers and the seeds removed.

We monitored all seeds collected in summer 2001 for insect emergence. Because no insect activity was detected by mid-March 2002, we dissected half of the seeds from each sample. Prior to insect emergence, attacked seeds often looked identical to unaffected seeds on the surface. We determined presence/absence of predation for each inflorescence by slicing into fully formed seeds and checking for larvae inside. Again, because dissection was halted for an entire sample when at least one seed was found to be infested, results are expressed as number of attacked shrubs rather than number of attacked seeds.

Post-dispersal Seed Predation

In the fall of 2001, 19 pairs of trays containing fresh seed were buried level with the soil surface at 19 random sample sites at Research Hill to estimate rates of post-dispersal seed predation. Each pair of 20-cm by 20-cm trays contained 3–4 cm of sand, covered with 1 cm of leaf litter, and 50 seeds mixed into the litter layer. The seeds used in this study were not tested for presence of insect larvae. They were collected from adult shrubs using seed traps during the summer of 2001, presumably reflecting similar densities, viability and insect infestation as seeds in the litter surrounding the trays. We covered one tray per pair with 0.5-cm by 0.5-cm wire mesh to prevent vertebrates from removing seeds and the other tray was left open. After 10 weeks and prior to the onset of the rainy season, the trays were brought back to the lab. Seeds not removed during the experiment were recovered by sifting through the sand and litter in the laboratory. Seed count data were analyzed using a paired *t* test.

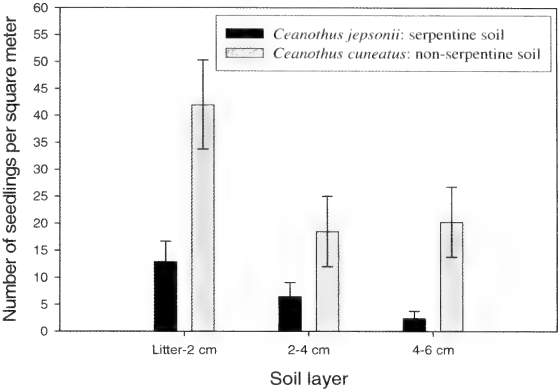


FIG. 1. Mean number (with standard error) of *C. jepsonii* and *C. cuneatus* seedlings to emerge in greenhouse soil layers, 2000 (*C. jepsonii* *n* = 31 per soil layer, except for 4–6 cm *n* = 25; *C. cuneatus* *n* = 31 per soil layer).

RESULTS

Seed Bank Structure

Ceanothus jepsonii seed density declined with an increase in depth down the soil column. We found a significant difference between each adjacent soil layer ($F_{1.77, 53, 18} = 4.26, P = 0.023$). There were few *C. jepsonii* seedlings to emerge overall (Fig. 1). The top layer, 0–2 cm, averaged 12.9 ± 3.7 seedlings/m². The two lower soil layers had even lower numbers of seedlings emerging (6.5 ± 2.6 seedlings and 2.4 ± 1.3 seedlings/m² respectively).

The non-serpentine soil containing *C. cuneatus* had significantly more seedlings in the top layer than in any other layer (42 ± 8.2 seedlings/m²), but seed density did not decline in a constant fashion down the soil column as in *C. jepsonii* (Fig. 1). The lowest layer, 4–6 cm down the soil column, had approximately the same number of seedlings on average as the middle layer, 2–4 cm (20.3 ± 6.5 seedlings/m² and 18.5 ± 6.5 seedlings/m² respectively). *Ceanothus cuneatus* seeds which were collected from non-serpentine soil had greater seedling emergence than *C. jepsonii*. Over three times as many *C. cuneatus* seedlings germinated in the top layer of soil as *C. jepsonii*.

Seeds in the Soil

Seeds with insect exit holes (i.e., preyed upon) averaged 525 ± 126 seeds/m² and intact seeds averaged 480 ± 127 seeds/m² in the soil seed bank (Fig. 2). No significant difference occurred with respect to density of the three seed types: preyed upon, intact and visibly inviable seeds ($F_{1.77, 14, 17} = 0.236, P = 0.77$). Intact seeds represented 34% of the total seeds; the two inviable categories combined for 66% of the total seed bank (Fig. 2). Because seeds that have been preyed upon are hollow and fragile, some were possibly destroyed during the sifting process.

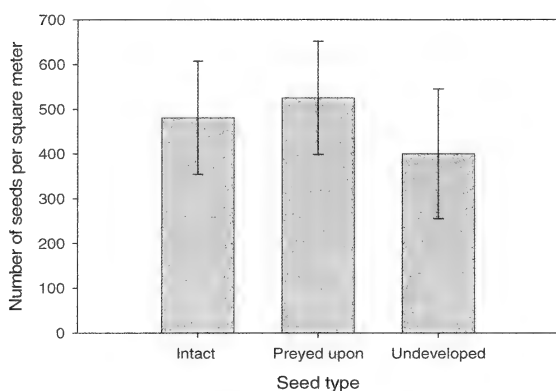


FIG. 2. Mean number of seeds (with standard error) recovered from *C. jepsonii* soil seed bank by seed type ($n = 9$). Proportions were statistically similar at 34% intact, 37% preyed upon and 29% undeveloped.

Seed Viability

A tetrazolium-chloride test showed that 91% of fresh seed (collected from shrubs and tested in the same season) was viable. The second batch, consisting of aged seeds recovered from the soil seed bank, showed only 63% viability.

Extent and Timing of Pre-dispersal Seed Predation

Of inflorescences exposed to the predator(s) for the entire flowering season, 37% were attacked. No inflorescences were attacked on or before April 11. All attacks occurred between April 22 and June 22 regardless of when the individual shrubs began to bloom (Fig. 3). The pre-dispersal seed predator(s) were active at the site and ovipositing during this time while seeds were still developing on the parent plant.

Plants were unable to escape predation through differences in flowering time. Early- and late-blooming cohorts had approximately the same number of shrubs attacked by the predator throughout the season. The two early-blooming cohorts showed four and five of 10 shrubs attacked respectively at each site. Four of the 10 late-blooming shrubs at Research Hill were attacked during the season. Early-blooming shrubs showed an increase in predation rates over the season, while late-blooming shrubs showed a mostly steady rate of predation after May 4 (Fig. 3). Some shrubs had only one inflorescence with beetle predation, while others had up to three of the five inspected inflorescences attacked. Inflorescences which were covered early on in the experiment had very low successful pollination rates with few or no seed/fruit developing and few remnant flowers left at the end of the season (80% and 60% for the first two treatments of early-blooming shrubs). It is probable that we were ineffective artificial pollinators and inflorescences covered later in the season with close to

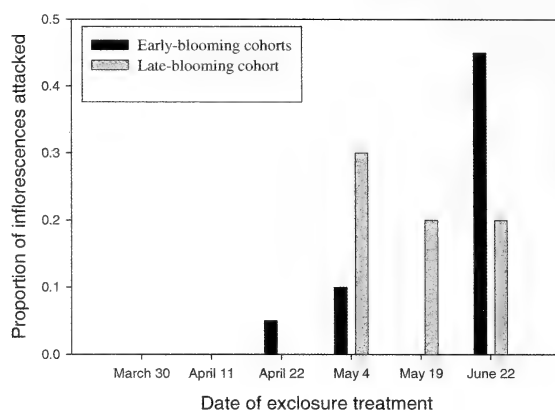


FIG. 3. Proportion of attacked inflorescences for early- and late-blooming cohorts throughout the season, 2001 (early-blooming $n = 20$, late-blooming $n = 10$). Plants were assigned to a cohort based on phenology. The date indicates when enclosures were installed on one of five branches of each plant. The early-blooming cohort did not receive a treatment on May 19.

100% seed production (with some aborted/undeveloped) had been pollinated by insects prior to enclosure installation.

Host Specificity and Distribution of Pre-dispersal Seed Predator

A beetle in the genus *Zabrotes* was found to be at least one of the pre-dispersal seed predators on *C. jepsonii* and *C. cuneatus*. Three beetles emerged from stored seeds (collected in 2000) and were identified by the USDA Systematic Entomology Lab, Beltsville, MD as belonging to *Zabrotes* (Coleoptera: Bruchidae: Amblycerinae). It is probable that there are more predators and/or parasites active at the site. The exit holes in the seeds and other evidence of attacks resemble those described by Furniss et al. (1978) and Huffman (2002) on *Ceanothus* seeds attacked by seed wasps. The larvae in the examined seeds were translucent, taking up the entire volume of the seed with no frass inside the seed. In some instances only one seed per fruit was attacked, in others all seeds appeared attacked. Some, but not all, fruits also had exit holes indicative of a seed wasp or weevil (Furniss et al. 1978).

Results from *C. cuneatus* showed that the pre-dispersal predator(s) are not just attacking *C. jepsonii*. At both the serpentine and non-serpentine sites, 30% of *C. cuneatus* inflorescences were attacked. Four of 10 *C. jepsonii* inflorescences collected from Butts Canyon Road site were attacked. During the 2001 blooming period, the proportion of shrubs attacked by the beetle appeared to be relatively homogeneous at different sites on different species (30–50%). Our study indicates that the pre-dispersal predator(s) are not restricted by host species or location.

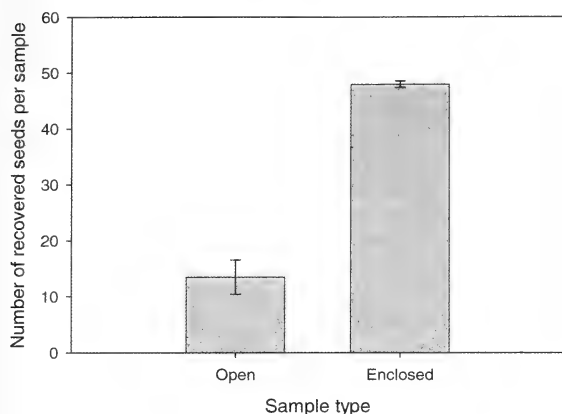


FIG. 4. Mean number (with standard error) of seeds recovered (maximum of 50) from open and caged samples following 10 weeks of exposure to post-dispersal predators, 2001 ($n = 20$).

Post-dispersal Seed Predation

Post-dispersal seed predation on *C. jepsonii* seeds was considerable. Significantly more seeds were removed from the open tray in each sample pair (t-test, $t = -11.080$; $df = 18$; $P = 1.77 \times 10^{-7}$). Open samples averaged 73% of seeds removed (36.5 ± 3.05) (Fig. 4). Enclosed samples averaged 5% of seeds removed (2.1 ± 0.57) after 10 weeks in the field.

DISCUSSION

Prior to germination and establishment, the critical life history stages of obligate-seeding *Ceanothus* species include seed development and survival in the soil seed bank. Several independent processes were found to reduce the potential number of *C. jepsonii* seeds in the soil seed bank. Pre-dispersal seed predators attacked at least 30% of the shrubs, post-dispersal predators removed over 70% of seeds in the litter, and 38% of the older intact seeds in the soil were inviable. A beetle in the genus *Zabrotes*, not previously known to oviposit on *Ceanothus*, was determined to be one of the causal agents of pre-dispersal seed predation. Other pre-dispersal predators at the site are possible, but were not identified during this study (Furniss et al. 1978; Huffman 2002). While *C. cuneatus* seed banks seem to retain more seeds than *C. jepsonii*, there is strong evidence for a host of removal vectors at different life stages for both species.

Seed density of *C. jepsonii* and *C. cuneatus* decreased with depth in the soil column as expected, as seeds are dispersed on the top layer of soil or litter and slowly are moved down the soil column by gravity, rain and soil movement by animals (Parker and Kelly 1989). Location in the soil is an important factor for seed germination because it affects the heat cue from fire; near the surface, temperatures may be too hot, but with increasing depth

are eventually too cool to stimulate germination. Overall germination rates were low for both species in our experiments, and we probably did not achieve maximum germination rates for either species. All montane *Ceanothus* species require a stratification treatment before they will germinate, and it seems that some coastal species of *Ceanothus* also have higher germination rates with even a brief stratification treatment (Quick and Quick 1961). Higher germination rates in low elevation *Ceanothus* species also have occurred with a stratification treatment, as in *Ceanothus cuneatus* from 762 m elevation (Quick 1935), and even in coastal species like *Ceanothus purpureus* from 500 m in Napa County (Garrett 2002).

However, in this experiment we were interested in relative location of seeds in the soil and a pattern is still discernible even without maximum germination rates. These data show that a high proportion of the seeds are in the top 2 cm of the soil column. Seeds that close to the surface may not survive the heat of a fire (Hasey 1985). A smaller proportion of seeds were found below 4 cm down the soil column which may be too low for germination to occur. *Ceanothus cuneatus* had two to three times more seed in the middle layer (2–4 cm) than *C. jepsonii*. More *C. cuneatus* seedlings emerged in all layers which may be a function of the shrubs being larger than *C. jepsonii* and producing more seeds, *C. cuneatus* responding more favorably without a stratification treatment, or predators preferentially attacking the larger *C. jepsonii* seeds. Flower and/or seed production rates were not examined during this study for either species, but are obviously crucial to understanding the dynamics of the seed banks of these species.

Pre-dispersal seed predation reduced the number of seeds entering the seed bank. Seeds with signs of insect emergence made up the largest proportion of *C. jepsonii* seeds recovered from the soil (37%). We documented attacks on at least 30% of *C. jepsonii* and *C. cuneatus* shrubs in and outside of the reserve. While in some species, insect damage can act as a cue for germination by breaking the seed coat (Hoffman et al. 1989; Ollerton and Lack 1996); this is not the case for *Ceanothus* because the predator destroys the entire seed.

Our study is the first documentation of *Zabrotes* attacking *Ceanothus* species. The genus *Zabrotes* normally feeds on members of the Fabaceae (Romero and Johnson 2000). Other beetle genera in the same subfamily have host records of species in the Rhamnaceae (Romero and Johnson 2000). Attacks by *Zabrotes* were found to occur late in seed development with no differences in attack rates between early- and late-blooming shrubs. A smooth seed coat, characteristic of *Ceanothus*, has been shown to be important for oviposition site selection for Bruchid beetles (Johnson 1981). Bruchids prefer to oviposit on relatively large seeds, which *Ce-*

anothus seeds are in comparison to most chaparral species (Moegenburg 1996).

Post-dispersal seed predators removed a significant portion of experimental seeds (>70% during a 10-week period). Seed density in these experiments approximated naturally occurring densities, and seeds were covered with small amounts of litter. We assume that rodents, birds or other vertebrates were responsible for the post-dispersal predation. However, ants may have also contributed to seed removal (caged samples averaged 5% of the seeds removed). The large reduction of seed density by post-dispersal predators is consistent with other experiments in chaparral (Keeley and Hays 1976; Evans et al. 1987; Mills and Kummerow 1989; Kelly and Parker 1990).

Undeveloped seeds accounted for approximately one-third of all seeds found in soil seed bank samples. These shriveled, hollow and obviously inviable seeds were undeveloped, and had no exit hole or other obvious signs infestation. Past studies have called this category 'aborted' (Hoffman et al. 1989; Zammit and Zedler 1993). They may have been seeds that never fully developed due to resource limitations; others may have been aborted due to predation by *Zabrotes* and/or other possible predators (Sallabanks and Courtney 1992) or been attacked by fungi after losing viability while in the soil. A high number of aborted seeds would be consistent with other studies of *Ceanothus* (Keeley 1977; Furniss et al. 1978; Huffman 2002). We also noted a high number of undeveloped seeds in the inflorescences inspected for pre-dispersal predation aside from those flowers that were unsuccessfully artificially pollinated by us.

The relatively small seed bank size compared to other chaparral genera, such as *Arctostaphylos*, is consistent with other studies of *Ceanothus* species (Keeley 1977; Schlesinger et al. 1982; Zammit and Zedler 1988; Parker and Kelly 1989; Zammit and Zedler 1993; Odion 2000; Garrett 2002). Intact seeds represented approximately one-third of seeds in the soil (480 ± 127 seeds/m²). Some seeds recovered from the soil exhibited worn seed coats, appearing scaly or discolored. Viability of the older seeds from the soil seed bank was 30% less than that of freshly collected seeds, suggesting a loss of viability over time. The more widespread, unrestricted species seems better able to utilize the strategy of producing many seedlings post-fire than the serpentine-restricted species that may be of concern for conservation of *C. jepsonii*. However, the seed losses documented here may simply be the mechanisms responsible for keeping soil seed bank numbers level over time rather than representing a recent decline due to new environmental factors and removal vectors (Keeley 1977, 1987a; Zammit and Zedler 1988, 1994).

Whether the current seed bank size and rates of seed removal reflect historic or natural levels is not clear in the context of recent anthropogenic influ-

ence such habitat fragmentation, species introductions and fire suppression. The seed losses, by native or non-native fauna, may be influencing the dynamics of the soil seed bank more than previously suspected. *Zabrotes* could not be identified to species, so more work is needed to determine whether it or the other potential pre-dispersal seed predators at the site are native to northern California. Pre-dispersal seed predation can alter the soil seed bank and the distribution of plants within their range (Louda 1982). As chaparral stands age, *Ceanothus* shrubs are often shaded out by larger shrubs or trees that invade these plant communities with a lack of fire (e.g., Keeley 1992; Zammit and Zedler 1994), further reducing seed input. Our findings suggest *Ceanothus* seed banks are quite dynamic and subject to a variety of seed removal and losses to seed input in a number of stages prior to germination.

ACKNOWLEDGMENTS

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7:30 p.m. on the 3rd Thursday of the month (except February)
2040 Life Sciences Building
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- September 8, 2005 Peter G. Kennedy, Department of Plant and Microbial Biology, University of California, Berkeley
http://ib.berkeley.edu/labs/dawson/research_othercalifornia.php
Ecological factors affecting tree encroachment in coastal California grasslands
- October 13, 2005 Gordon W. Frankie, Department of Environmental Science, Policy and Management, University of California, Berkeley
<http://espm.berkeley.edu/directory/fac/frankie.g.html>
Native California bees and their native California host plants in urban environments
- November 10, 2005 Matteo Garbelotto, Department of Environmental Science, Policy and Management, University of California, Berkeley
http://espm.berkeley.edu/directory/fac/garbelotto_m.htm
The dangerous liaisons: an overview of how man can unwittingly introduce microbes capable of forever changing our natural ecosystems
- February 11, 2006 **Annual Banquet, Rancho Santa Ana Botanic Garden, Claremont, CA**
Jon Keeley, Sequoia and Kings Canyon Field Station, USGS, Western Ecological Research Station, Three Rivers
<http://www.werc.gov/seki/keeley.asp>
Ecology and Evolution of Fire Prone Ecosystems in California
- March 9, 2006 Todd Keeler-Wolf, Wildlife Habitat Data Analysis Branch, California Department of Fish and Game, Sacramento
<http://www.ucpress.edu/books/pages/1270001.html>
The value of vegetation sampling, classification, and mapping for plant ecology and conservation in California
- April 13, 2006 Mark S. Brunell, Department of Biological Sciences, University of the Pacific, Stockton
<http://www1.pacific.edu/cop/biology/home.htm>
Origin and relationships of the Brazoria Palmetto (*Sabal*) based on AFLP markers

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Information and reservation forms for the annual banquet will be mailed to Society members.
For further information about lectures, banquet registration forms, activities or membership, please call 510/643-7008.

DIGITIZATION OF A HISTORIC DATASET: THE WIESLANDER CALIFORNIA VEGETATION TYPE MAPPING PROJECT

MAGGI KELLY¹ AND BARBARA ALLEN-DIAZ

Department of Environmental Sciences, Policy and Management, 137 Mulford Hall, #3114, U.C. Berkeley, Berkeley, CA 94720-3114

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ABSTRACT

In the 1920s and 1930s Albert Everett Wieslander and several others explored much of California's wilderness sampling vegetation, taking photographs, collecting specimens, and drawing detailed maps of what they found. The collection is now known as the Wieslander Vegetation Type Mapping (VTM) collection, and the entire survey encompassed nearly seventy million acres of the state, covering most of the wild areas exclusive of the deserts and the larger agricultural areas. These data represent a valuable resource for comparative and conservation ecology. We are digitizing the entire project, and making it available to researchers and the public. The current "VTM Digitization" Project, as it is known, is described in this article, and is a collaborative effort by teams at University of California Berkeley and University of California Davis, funded by the U.S. Forest Service and U.S. Department of Agriculture's Cooperative State Research, Education and Extension Service. The VTM Digitization Project aims to digitize the entire VTM collection for use in ecological and geospatial analyses, and to facilitate access and distribution of the data by researchers and interested parties. This article describes our efforts at making the VTM plot data, maps and photographs digital, spatially referenced, readily available, and web-accessible via an Internet-based Geographic Information System (webGIS) application. In addition, we discuss potential uses for the data and caveats associated with its use, particularly spatial accuracy.

Key Words: VTM dataset, webGIS, digital database, California plant communities.

The 18th through early 20th century was a time of tremendous exploration of the landscape of the United States, and the data generated by these surveys include information about pre- and early settlement vegetation. The Public Land Survey System (PLS) which began in 1785 with the Land Ordinance Act is probably the best known example (Iverson 1988; Buisseret 1990; White and Mladenoff 1994; Manies and Mladenoff 2000; Manies et al. 2001), but there are others, including numerous 18th and 19th century land surveys, settlement maps, and deeds (Siccama 1971; Russell 1981; Foster et al. 1998). While these efforts were land surveys rather than botanical ones, valuable vegetation data are contained in these collections, and in many states, they provide the first statewide vegetation map showing the natural environment before extensive changes associated with European settlement. Many researchers are now interested in these collections, recognizing their importance for historical ecological research, as well as to establish baselines for analyzing current patterns of land use change (Galatowitsch 1990; White and Mladenoff 1994; Minnich et al. 1995; He et al. 2000; Schulte et al. 2002). As an example, Schulte and Mladenoff (2001) claim that the PLS records provide the

"broadest coverage (Ohio to the west coast) and finest spatial resolution (one square mile) of any pre-settlement data source".

Although there are numerous examples of coastal maps of California dating from the 16th century, surveying of the land from the Mexican border northward did not begin until the early 19th century (Heckrotte and Sweetkind 1999), and statewide mapping endeavors began in earnest in the mid-19th century with statehood. The California PLS survey began shortly after 1851, and the data collected included hydrography, vegetation, and natural resources, as well as cultural details (Buisseret 1990; Heckrotte and Sweetkind 1999). Further statewide efforts at mapping the natural landscape followed, including an effort by the California Geological Survey at statewide biological resource mapping in the 1860s (Erter 2000). The effort was abandoned in 1873 as a result of several factors, including politics, personnel, and poorly estimated costs.

Following these efforts, Albert Everett Wieslander and several others, with funding from the Forest Service and other federal, state and county agencies, began mapping California's vegetation in an effort that was described later as the most important and comprehensive botanical map of a large area ever undertaken anywhere on the earth's surface (Jepson et al. 2000). The Wieslander crew explored much of California's wilderness sampling vegeta-

¹ Author for correspondence, email: mkelly@nature.berkeley.edu

TABLE 1. SOME POTENTIAL USES OF THE VTM DATASET.

| Data type | Dataset content | Potential uses |
|-----------------|---|--|
| Plot Data | 18,000 plots | —Quantitative analysis of vegetation change at landscape or larger scales. |
| Plot Maps | 150 15- and 30-minute USGS topographic quadrangles | —Use in relocating plots for analysis of disturbance: e.g., historic forest stand structure in forests across a gradient of Sudden Oak Death infestation. |
| Vegetation Maps | 350 15- and 30-minute topographic quadrangles | —Retrospective mapping to examine vegetation alliance changes. |
| Photographs | 3100 black and white photographs | —Compare mapping methods in key areas such as Yosemite, examining e.g., average size of polygon, minimum polygon, and number of different mapping units. —Graphic examples of land-use change from stand to landscape-scale. —Evidence of disturbance (e.g., fire, logging). |

tion, taking photographs, collecting specimens and drawing detailed maps (Wieslander 1935b; Colwell 1977). The natural vegetation mapping was carried out by the U.S. Forest Service (USFS) California Forest and Range Experiment Station in Berkeley (Colwell 1977). Mapping continued using a protocol developed by Wieslander until it was stopped during World War II. By then, 16 million ha had been mapped (Wieslander 1961; Colwell 1977). The well-preserved collection is now known as the Wieslander Vegetation Type Mapping (VTM) collection, and the entire survey encompassed nearly 28 million ha, covering most of the state's natural areas exclusive of the deserts and the larger agricultural areas. The collection represents a fascinating snapshot of California vegetation in the early part of the last century, and represents a valuable resource for foresters, ecologists, land managers, and others interested in the natural environment of early 20th century California, and land use changes since then. For example, the collection has been used in part as a basis for the statewide California Gap Analysis maps produced decades later (Davis et al. 1995; Walker 2000).

We are digitizing the collection, and making it available to researchers and the public. The current "VTM Digitization" Project is a collaborative effort by teams at University of California Berkeley (UCB) and University of California Davis (UCD), funded by the USFS, and U.S. Department of Agriculture Cooperative State Research, Education and Extension Service (USDA CSREES). The VTM Digitization Project aims to digitize the entire VTM collection for use in ecological and geospatial analyses, and to facilitate access and distribution of the data by researchers and interested parties. This article describes our efforts at making the VTM collection digital, spatially referenced, readily available, and web-accessible via an Internet-based Geographic Information System (webGIS) application. In this paper we aim to: 1) describe the collection, 2) alert readers to the digitization project, 3) describe the methods used to complete the digitization, and 4) discuss the potential uses for the

data, as well as some of the caveats in using the data.

The Vegetation Type Mapping (VTM) Collection

The VTM collection consists of five components, four of which are described here: 1) Plot data gathered on more than 18,000 plots around the state that include floristic and environmental detail, 2) Plot maps depicting the locations of plots sampled, 3) Vegetation maps, showing hand drawn polygons of forest types, and their associated species, and, 4) Landscape photographs and associated information about location and content of the photographs. The team also collected herbarium specimens for every species recorded on the vegetation maps or in the sample plots (Ertter 2000). We have not begun incorporating the herbarium specimens into this digital collection, but we are providing a link between our webGIS system and the Jepson Herbarium Specimen Catalog.

Plot Data

There are approximately 18,000 plots statewide, concentrated primarily along the central and southern coastal ranges, and along the Sierra Nevada. These plots were surveyed not only as a check on the vegetation mapping, but also to survey the diversity of California vegetation types for details such as species composition, size and stand density of trees and shrubs and depth of leaf litter. These sample plots were located across a gradient of vegetation types, and the historic records contain data regarding tree stand structure (number per diameter class), percent cover of dominant overstory and understory vegetation by species, soil type, parent material, leaf litter, elevation, slope, aspect, parent material, and other environmental variables.

Details of the plot design are as follows (Wieslander 1935a; Wieslander 1935b). Each plot was rectangular in shape with the longer axis running upslope. The plots were 800 m² in size in forests, and 400 m² in scrub and chaparral communities. For example, the 400 m² plots were laid out using

two chains (ca. 40 m) long and one-half chain (10 m) wide, and divided into 100 squares (ca. 4 m²). In both types of plots, the dominant species within each milacre was recorded. When less than 50% of the square was vegetative cover, ground surface characteristics such as bare ground, rock outcrops or tree trunks were noted. A summary of the squares within the rectangle plot was provided, noting the average height of the dominant species (to the nearest 0.5 ft or 15 cm). At the same time, trees greater than 10 cm in dbh within 10 m of either side of the center-line were tallied by species and diameter class. In both types of plots, additional information such as slope, soil character and year of last burn was recorded (Wieslander 1935a; Wieslander 1935b).

All plot data was stored on paper data sheets, and individual plots were numbered according to U.S. Geological Survey (USGS) topographic quadrangle map name, quad section number and plot number. There are about 150 original maps remaining in the

collection. A snapshot of the plot data is found in Figure 1a.

Plot Maps

The VTM plot maps show the locations of all the individual plots surveyed by the original VTM crews. Hollow circles of about 3.5 mm in diameter depicting the location of the plots were stamped in red ink on USGS topographic maps (editions of 1893–1920, reprinted in the 1930s) that had been cut into sections, mounted on canvas, and folded, to facilitate use in the field. This allowed for repeated folding along the seams, without loss of mapped information. Unfortunately, the resulting maps were not dimensionally stable, and 80 years of use, temperature extremes, and other factors have warped many of the plot maps. This has required us to take steps in the georeferencing process to reduce these errors, described below. The plot map collection comprises about 150, 15-minute (1:62,500 scale) and 30-minute (1:125,000

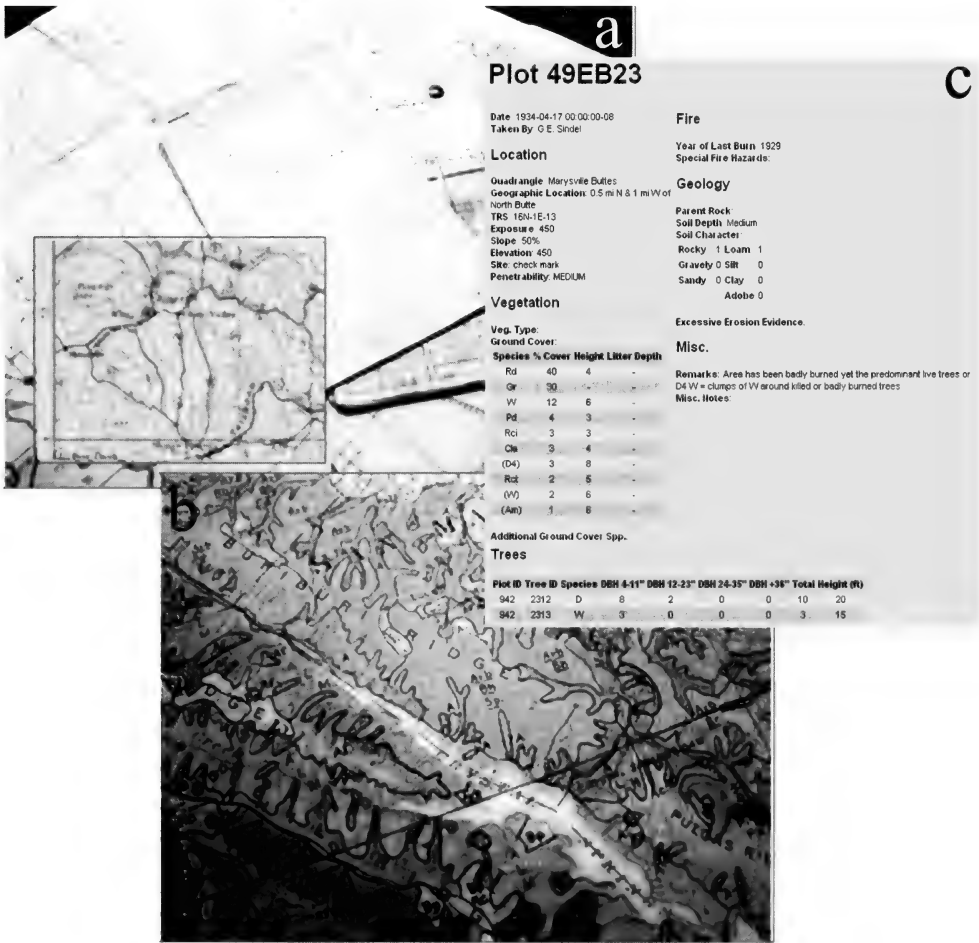


FIG. 1. Plot and vegetation map data examples: a) scanned plot maps and plot data sheets, b) a sample vegetation map, and c) a sample of the database return for one plot.

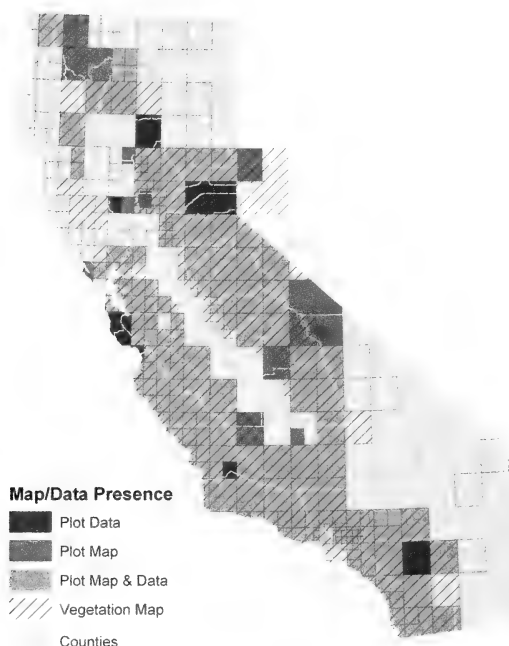


FIG. 2. Inventory of VTM plot maps in California. We have produced inventory maps for other parts of the collection. These can be found at: <http://vtm.berkeley.edu/>

scale) USGS quadrangles, primarily concentrated along the central and southern coastal ranges, and along the Sierra Nevada. Figure 2 displays our inventory of the plot maps and Figure 1a shows an example of the plot maps and data sheets.

Vegetation Maps

The vegetation type maps were mapped in the field by VTM crews, directly upon 15-minute (1:62,500-scale) topographic quadrangles by direct observation, and “sketching from ridges, peaks, and other vantage points”, and supplemented by sample plots (Wieslander 1935b). With average conditions, it took a two-man crew from six to eight weeks to complete the field work for a 15-minute quad of about 6,070 ha (Wieslander 1935a). Plant communities were mapped to a minimum of 16 ha (Colwell 1977). Dominant plant species were mapped, while understory vegetation information was collected in the sample plots. The vegetation mapping scheme, since it was done in the field via overlooks and remote vantage points was by necessity driven by overstory species recognition (i.e., “the dominant vegetation visible externally” (Wieslander 1935a)). The VTM method used two vegetation classification concepts: they mapped “mosaic types” which are complex vegetation conditions that result from fire or other disturbances, or pure and mixed stand conditions which they associated with natural plant associations (Wieslander 1935a).

The mapped products include map sheets over-

printed in color on 15- and 30-minute USGS topographic quadrangles, and simplified, uncolored blue-line print sheets. Some areas of the state have “zoomed-in” vegetation maps drawn on 6- and 7.5-minute USGS quads. The major vegetation types are shown in different colors and separated by ink lines (Colwell 1977). These are further subdivided on the map into pure and mixed stands, with notation on species composition. The teams used a protocol designed to be useful for engineers, foresters, and managers, and attempted to group vegetation types by their fire hazard characteristics, uses, or economic importance.

There are about 330 of these detailed maps in the collection, covering about 16 million ha. Some were published, and some remain unpublished. Figure 1b shows an example of a vegetation map from the San Mateo area. The plot data sheets, plot maps, and vegetation maps are currently curated by Dr. Allen-Diaz in the Environmental Sciences, Policy and Management Department in the College of Natural Resources at UCB.

Photographs and Associated Data

There are approximately 3100 black and white photographs (9.2×13.6 cm) from 1920–1941, and approximately 100 color topographic maps. Many of the photographs are keyed to USGS topographical maps. For these photographs, the location of the place where the photos were taken is written in red pen on the maps, with an arrow marking the vantage point and view of the photo. Some of the photographs are “panorama” style images, but most are focused on a stand (see examples in Fig. 3). The photographs document the typical and atypical subtype, wider species, timber stand conditions, range of variation, and consequences of land use and cultivation, grazing, logging, mining and fire. The main photographer was Albert Wieslander. A second “series” was done by Richard C. Wilson, a UCB School of Forestry graduate. Several other photographers, including C. Raymond Clar, participated in the project. The Marian Koshland Bioscience and Natural Resources Library at the University of California, Berkeley houses the VTM Photographs Collection.

METHODS AND RESULTS TO DATE

Initial Preparation

In order to create a complete and linked database accessible to the public and to researchers, we needed to make all parts of the collection digital, index each component by its spatial location, and develop a web tool for users to query, view, and download data from the database. These are described in turn here. Similar efforts have been made in other states (e.g. Iowa and Wisconsin) with interesting results (Anderson 1996; Schulte et al. 2002). We refer to some of the lessons learned in

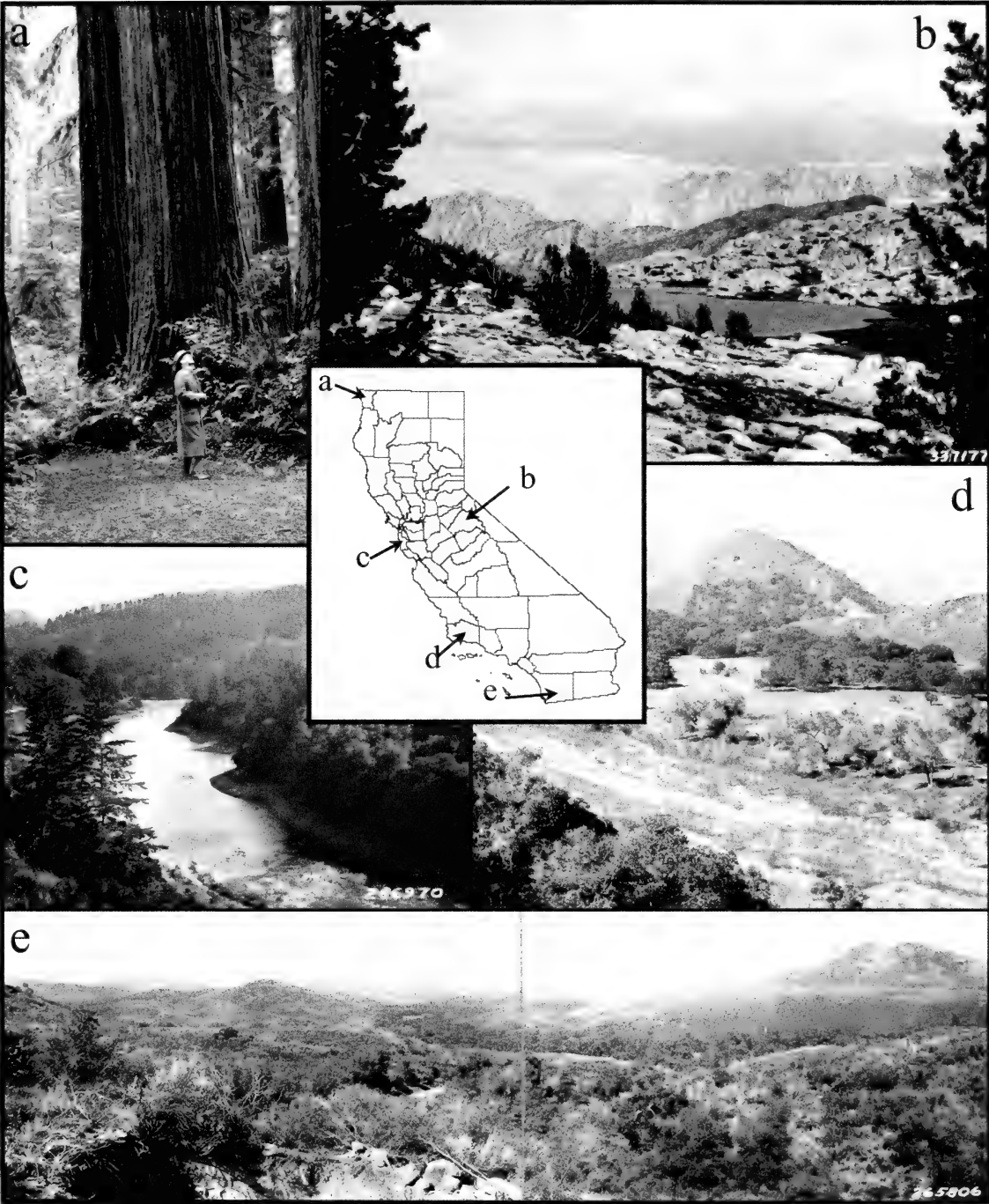


FIG. 3. Representative photographs from the original VTM collection (all photographs taken by A. E. Wieslander, and descriptions from photograph captions): (a) In Mill Creek State Park, Del Norte County, showing coastal redwood and R. D. Garver, taken 11/1/1940; (b) Snow Lake in Tuolumne County, showing whitebark pine and associated ground cover, taken 8/1/1936; (c) In San Mateo County, showing east arm of Pilarcitos Lake, with Douglas fir, coast live oak, madrone and California bay woodland and coastal sagebrush, taken 7/24/1932; (d) Looking southwest down Cuyuma Creek in Santa Barbara County, showing coast live oak woodland and *Salvia leucophylla*; taken 4/5/1936; and (e) Panorama looking north and northeast showing Long Valley Peak and Oak Valley in San Diego County, showing coast live oak woodland with scattered Jeffrey pine and Engelmann oak woodland on upper left slope, taken 4/4/1931.

those projects, and others utilizing historic vegetation data.

Plot database. Many researchers have used the VTM collection for research (Bradbury 1974; Minnich et al. 1995; Vayssieres et al. 2000; Franklin et al. 2004; Taylor 2004b), and some of these people have made portions of the VTM plot data digital. Allen-Diaz produced the largest database containing about 4,000 plots, as part of a statewide oak woodland classification effort (Allen et al. 1989). We collected existing electronic versions of VTM plot data and merged them into a standardized database; now we are in the process of entering all remaining plot data into this common database (Fig. 1c). Once completed, each plot will have a unique identifier, based on its quad, the section of the quad, and its unique number in that section. This identifier will geographically locate the plot, and link the plot location with the database for future analysis.

Plot maps. All plot maps have been scanned at 600 dpi, one cut segment at a time. Uncut, scanned versions of each USGS topographic map of the same edition and reprint were searched for in several California map libraries and spatial data clearinghouses. To date, we have found more than half of the maps in an uncut state in either the UCB Map Library, the California State University Chico Meriam Library California Historic Topographic Map Collection, the Los Angeles County Historical Topographic Map Collection, or the map library at the University of California Santa Barbara.

These uncut maps are used in the georeferencing process. Georeferencing is the process whereby a map or set of maps is referenced to true world coordinates through the collection of "tie points" (Jensen 1996). The tie points are used to position two images coincident with each other through a geometric transformation that translates the location of each tie point on the historic map to that found on the modern reference map. A root mean squared error (RMSE) is then calculated to estimate overall accuracy of the transformation. Others have attempted this process with the VTM maps. For example, Walker (2000) used modern satellite imagery as the reference map in the georeferencing process. In this case, we first registered the historic uncut maps of the same vintage as the VTM cut maps to modern maps (1:24,000-scale USGS Digital Raster Graphic digital images of modern USGS quadrangles) of a known projection and coordinate system using stable tie points such as roads and peaks. We used between eight and 16 tie points per map. Next, the uncut scanned VTM maps were georeferenced to the georeferenced historic uncut maps using common map features as the tie points. We used a minimum of six tie points per segment. We used first order polynomial transformations for each step. All georeferencing used Erdas Imagine 8.7 software (Leica 2004), and ArcGIS software

(ESRI 2004). Average RMSE for the process was around 60 m. We have performed some preliminary examination of this error, and our results suggest that age of base map is one critical factor in determining error contribution; basemaps made before 1911 have larger RMSE values; and a second important contribution is elevation: maps on lower elevations have less RMSE.

Vegetation maps. The vegetation maps are also being scanned and georeferenced using the same protocol as the plot maps. The vegetation maps have not all been cut into sections, and can be scanned and georeferenced in their entirety. Associated metadata from each vegetation map is collected at the time of scanning. This component of the project is being completed by Jim Thorne and Jeff Kennedy at UCD.

Photograph collection. The Library Photographic Services is digitizing the photograph collection. Each photograph is scanned, and information from its captions has been entered into an Access database, which will be available on the Library Web. Once the project is complete, users will be able to search by keyword, genus and species, and quad name. Data from the caption include a brief description of the location and subject of the photograph including relevant genus and species, and quad name. The photographer, date of the photograph, and occasionally township and range are included. In addition, researchers will be able to search for the photographs using the webGIS tool described below.

Website development. We have developed a website to update interested parties on our progress. The website is currently available at: <http://vtm.berkeley.edu/>. Here you can find program progress, inventory maps and other information, including our "webGIS" application that unites all aspects of the project. WebGIS is a new term that refers to websites that unite two components: (1) GIS database storage and maintenance and (2) Internet accessibility. Although not yet widely used in natural resource management, such systems are a promising option for entering and storing heterogeneous datasets, indexed by location, and making them widely available in a visual, dynamic and interactive format (Kearns et al. 2003). When finished, the website will allow users to view all data associated with the project in mapped form. Users will be able to turn on and off different "layers" of data (e.g., modern vegetation, elevation, or VTM plot map quads), zoom in and out, viewing increasing detail as they zoom in, search for particular areas of interest by entering quad name information, or geographic coordinates, view photographs tied to the location, query the plot database, create their own maps, and finally, request the data itself for research purposes.

Figure 4 shows plot maps, and plot locations overlaid on modern topographical data. Once the en-



FIG. 4. VTM plots in the San Francisco Bay area. The original, scanned and georeferenced plot maps from the VTM collection are superimposed on a modern elevation map. Red circles depict locations of VTM plots.

tire collection has been digitized, we will be able to provide this kind of seamless digital view for the entire collection.

DISCUSSION

Potential Users and Uses of the Data

There are many potential users and uses for the data in this collection. Wieslander spent consider-

able time thinking about the uses of these data in the future; and claimed that “the data not only serve as a basis for mapping sites in the field but also are suitable for scientific study later” (Wieslander 1935a). He outlined some potential uses for the data in Madroño in 1935 that still hold true today. He wrote the data might provide: 1) a partial explanation of the present distribution of vegetation types and dominant species; 2) a better understand-

ing of vegetation changes that have occurred in the past, those now in progress, or those to be expected to occur in the future; 3) further contributions to our knowledge of the values of certain plants and vegetational types as indicators of particular soil and climatic conditions; and 4) suggestions for future investigations and also a foundation for further research. He also provided explanations of change that might be controversial today: "the most striking and significant of such changes are those representing a progressive deterioration from higher and more valuable to lower and less valuable types of vegetation as a result of such land abuse as destructive logging, accidental and willful summer fires, the practice of annual burning in many foothill and mountain localities, and excessive grazing" (all quotes from Wieslander [1935b]).

The VTM methods and resulting data lend themselves to modern ecological research, and to date the data have been used in three broad areas of inquiry. First, the data have been used to classify vegetation communities in the state (Jensen 1947; Griffin and Critchfield 1972; Allen et al. 1989; Allen et al. 1991; Allen-Diaz and Holzman 1991). The detailed collection and recording of floristic and environmental detail at the plot scale allows for *a posteriori* determination of vegetation types by researchers (Walker 2000), making the data more useable and flexible for modern ecologists. This approach was used by Allen-Diaz et al. (1989) in creating a comprehensive classification scheme for California's hardwood rangelands, which in turn was used in the manual of California Vegetation (Sawyer and Keeler-Wolf 1995). The data have also been used to validate modern models of vegetation composition (Vayssières et al. 2000; Franklin 2002). These efforts assume a static vegetation composition over decades at a large scale (e.g., Franklin (2002) examined a 3880 km² study area).

Secondly, the decades-old collection of plot data has also been used in reconstructing California vegetation conditions in the early 20th century in order to examine changes due to disturbances such as fire and disease, or to examine local trajectories of land cover change. Bradbury (1974) was perhaps the earliest published example of this. He examined 40 years of change in San Diego County vegetation, and found little change in the area, most of which was clearly disturbance-related (Bradbury 1974; Franklin 2002). In contrast, other researchers found significant changes in species composition. For example, Minnich et al. (1995) used VTM data to document significant shifts in species composition and stand density in the San Bernardino Mountains of California, and discussed the role of fire in changing the forests in California conifer forests. Taylor (2004) relocated 78 VTM plots in San Diego County, and discovered that while overall shrub cover loss was less than reported in a comparable area (Riverside County), there was a shift in composition in several shrub communities in the San

Diego County area (Taylor 2004b). These studies that relocate VTM plot data and compare plant abundance and distribution measures with current data might be more successful in certain vegetation types; for example, areas with trees or with less diversity might be more amenable to comparative analyses. Efforts over larger scales also should be encouraged, as successful relocation of individual plots can be problematic (Keeley 2004).

Finally, the vegetation map portion of the VTM collection has also been put to use. Walker (2000) compared the VTM vegetation maps and other historic sources of vegetation distribution in Yosemite National Park with modern sources of mapped vegetation data to examine decadal changes across the Park. Such retrospective mapping projects are not without challenges: the original inclination of the VTM design was forestry-based, with a vegetation classification scheme developed for the project and designed for further forestry applications. In addition, the vegetation mapping was done via remote vantage points. These choices necessarily resulted in large minimum mapping units and a classification scheme based on overstory canopy dominance. Modern ecologist wishing to examine vegetation changes through these maps should be cognizant of these facts. Indeed, these kinds of considerations are also necessary in comparing different contemporary vegetation datasets (e.g., Manual of California Vegetation Classification and the USFS's CalVeg dataset (Thorne et al. 2004).

We are interested in using the collection to compare current stand structure and composition with 70–80-year-old stand structure in areas affected by the new forest disease called "Sudden Oak Death" (Rizzo and Garbelotto 2003). We hope to understand why there is such a patchy distribution of infection in forests with Sudden Oak Death. We intend to look at interrelationships between land use changes, climate changes, pest invasions, stand growth, and infection, and model change in plant community composition and structure. This project is one example of a multi-scaled approach to historical ecology: it utilizes plot level information on current vegetation community structure across a gradient of sites with infected trees, and historical vegetation data at a larger-scale to examine possible explanations for the patchiness of the disease statewide.

Spatial Accuracy Considerations

Re-locating plots from historic maps is recognized by many to be a challenge (for some the greatest challenge) facing modern ecologists using these data. Several researchers have discussed caveats associated with use of historical ecological data, and recommended caution in using older collections. Indeed, the use of PLS data for historical ecology has been controversial because of possible inconsistencies caused by surveyor variability (Gal-

atowitsch 1990). While Schulte and Mladenoff (2001) and Siccama (1971) found that surveyors were consistent in recording distance and direction to witness trees, they also note that surveyors were not consistent in describing species and diameter characteristics, possibly due to seasonality of sampling (Schulte and Mladenoff 2001). In addition, several researchers note variability among surveyors across species, diameter, size and location (Bourdo 1956; Galatowitsch 1990; Manies et al. 2001; Schulte et al. 2002). Overall, however, Manies and Mladenoff (2000) found the PLS method accurately estimated relative species composition and the order of dominance of land cover types at broad spatial scales.

These experiences are applicable to the use of the VTM collection, although surveyor inconsistencies might be less than in the PLS collections as a result of a smaller project, more modern equipment, and perhaps a better-trained staff. Indeed, Minnich et al. (1995) describe confidence in locating plots within a 100 m radius by reference to fixed features such as roads, and the location of prominent trees included in the original dataset (Minnich et al. 1995). In addition, they took three replicates at each plot, to ensure that they had located the plots. Walker (2000) found that while the overall fidelity of species composition mapping was good, the spatial accuracy of the plots (and of vegetation polygons) varied with topography, and spatial error increased in areas of high terrain (Walker 2000). Franklin (2002) found discrepancies between the VTM data and the more modern USFS Forest Inventory and Assessment (FIA) plots over a large area, but proposes that this might be a result of differing sampling schemes between the VTM and FIA plots, not a result of spatial accuracy.

A less optimistic view is presented by Keeley (2004). He found considerable spatial variability in coastal sage scrub and chaparral communities in Southern California. Consequently, he maintains that the accuracy and precision to which VTM plots in chaparral might be relocated is not sufficient to perform plot-by-plot analysis of community change. In other words, when using VTM data on a plot-by-plot basis in chaparral communities, any change found might be an artifact of errors in plot re-location, and not indicative of real change. This is a reasonable argument for chaparral communities, but many authors contend that in forested communities the problem of relocation might not be as severe due to the existence of persistent trees, as described above.

Plot relocation still remains an important challenge in ecological research with these data. We estimate that our georeferencing technique generates plot locations with a combined error of around 200 m on a 15-minute (1:63,500-scale) quad. The plot markings on the original maps constitute the largest component of this error. These plots markers are 3.5 mm in size, generating circles with radii

equivalent to 110 m on the ground when using a 15-minute (1:63,500-scale) map. In addition, the georeferencing process contributes an additional 60 m error (based on the average RMSE for the process, reported in Erdas Imagine). Finally, we need to include the error contributed by the original USGS map itself, which is about 30 m (USGS 1947). We have combined these sources to generate an overall error of about 200 m per plot, which is similar to that reported by Walker (2000) using a different georeferencing method. This amount is in excess of any error in locating the original plot on a quad by the VTM crew in the field. The overall error might be lessened through use of the slope and aspect values recorded in the plot data in comparison with topographic data from a modern Digital Elevation Model (Taylor 2004a).

CONCLUSIONS

California's landscape is complex, varied and extremely dynamic, and in the 20th century has experienced numerous agents of large-scale change. Fire, urban and exurban development and expansion, harvesting, invasive species, and new forest diseases such as Sudden Oak Death combine to alter the environment in ways that could not be imagined 80 years ago when Weislander was working. Yet, the legacy that he and his crews have left us, a detailed and accurate picture of California vegetation of that time, help us to understand change, and better manage it for the future. Clearly, the ability to relocate plots with sufficient precision and accuracy for detailed historical analysis will remain an important challenge in historical ecology, but we contend that researchers using historical data have found a range of approaches that address this and make the dataset valuable for ecological research. For example, in areas of little change, the floristic detail of the plot data can support vegetation community classification, or validate new models of species distribution. In areas of change, researchers have pursued landscape and larger scale analysis of historical data, combining several plots and examining changes across watersheds, regions, or even states.

The kind of data repository we are building will provide valuable data and tools for those interested in California's changing vegetation through the 20th century and beyond. We hope to have the data accessible to researchers by Fall 2005 at vtm.berkeley.edu.

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and Natural Resources Library at UC Berkeley; and Jeff Kennedy and Jim Thorne from UC Davis. Without all these people, this collection could not have been brought to life again. We are grateful for the insightful comments from three reviewers; incorporation of these reviews greatly strengthened this paper.

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A NEW SPECIES OF *STREPTANTHUS* (BRASSICACEAE) FROM THREE
PEAKS IN LAKE COUNTY, CALIFORNIA

RICHARD O'DONNELL

1317 Cornell Avenue, Berkeley, CA 94702

REBECCA W. DOLAN

Friesner Herbarium, Butler University, 4600 Sunset Ave., Indianapolis, IN 46208
rdolan@butler.edu

ABSTRACT

Streptanthus vernalis is a newly described species inhabiting serpentine rock outcrops in the Three Peaks area in Lake County, California. Morphological and allozyme data indicate that this taxon is related to the *S. morrisonii* complex.

Key Words: *Streptanthus*, serpentine, endemism, new species, allozyme analysis.

In the 1970s and 1980s, botanical researchers who were developing information about the distribution of *Streptanthus morrisonii* F.W. Hoffman subsp. *elatus* F.W. Hoffman observed an undescribed jewelflower near Three Peaks in Lake County, California, USA. Their findings were not published. In this paper, we describe and name this jewelflower and provide the findings of allozyme analysis that indicate the relationship of the new species to morphologically similar species in the region.

SPECIES TREATMENT

Streptanthus vernalis Richard O'Donnell and Rebecca Dolan, sp. nov.—TYPE: USA, California, Lake Co., serpentine talus and gravel less than 0.4 km northeast of Three Peaks, Lake County, California, along an abandoned fire trail between White Point and McGuire Peak. UTM 10 537004E 4282565N (WGS84/NAD83). USGS Detert Reservoir Quad. 610 m elevation. *Richard O'Donnell s.n.* (Holotype: JEPS). Collected May 1, 2004.

Herba annua omnino glabra; caules erecti simplices vel ramose, 2–20 cm alti; folia pauca, plerumque basalia crassa subtus purpurea, supra viridia, 3–4 cm longa; folia inferiora orbiculata vel obovata, saliete crenata, petioles 1 cm longa; folia superiora sessilia, lineri-lanceolata, integra; flores erecti; sepala 6–7 mm longa, viridia apicibus patentibus acutis; petala valde exserta, alba, 2 mm longa; stamina trisericata, superiorum filamentis 7–8 mm longis, connatis; siliquae 4–5 cm longae, erectae, torulosae, ascendentis; semina alata.

Annual. Stem erect, simple or branched, 2–20 cm tall. Leaves few, mostly basal, thick, purple beneath, green above, 3–4 cm long, lower leaves orbicular to obovate, saliently crenate, petioles 1 cm long, upper leaves sessile, linear lanceolate, entire. Flowers erect. Sepals green, tips reflexed, 6–7 mm

long. Corolla flask-shaped. Petals well exserted, equal, recurved, white, 2 mm long. Stamens in three pairs, upper pair 7–8 mm long, filaments exserted, connate to the apex, anthers reduced, reflexed at anthesis, middle pair connate ½ of length, lower pair free. Stigma entire. Silique 4–5 cm long, ascending, torulose. Seeds orange, winged.

Streptanthus vernalis is found in serpentine talus and gravel less than a quarter of a mile northeast of Three Peaks, Lake County, California, along an abandoned fire trail between White Point and McGuire Peak. Plants in the vicinity of the small colony include *Cupressus sargentii* Jepson, *Pinus sabiniana* Douglas, *Arctostaphylos viscida* C. Parry, *Quercus durata* Jepson, *Streptanthus morrisonii* subsp. *elatus* F. W. Hoffman, *Mimulus brachiatus* Pennell, *Minuartia douglasii* Torrey and A. Gray, and *Epilobium minutum* Lehm.

Several rare serpentine endemics occur near Three Peaks, including *Harmonia hallii* (D. D. Keck) B. G. Baldwin, *Cryptantha hispidula* Brand, *Triteleia peduncularis* Lindley, *Hesperolinon spergulinum* A. Gray, and *Solidago guiradonis* A. Gray. Three Peaks is most notable as the type locality for *Streptanthus morrisonii* subsp. *elatus*, discovered there by Freed Hoffman in 1952.

MORPHOLOGY

Neilson first reported an undescribed *Streptanthus* in an unpublished consultant's report (Neilson 1977). He referred to this undescribed taxon as a diminutive variety of the generally much taller *S. morrisonii* subsp. *elatus* and noted that it was fairly common in the vicinity of Three Peaks, an observation we have not been able to confirm. His research also located two herbarium specimens at the Dudley Herbarium (DS) and the California Academy of Sciences (CAS) that he believed were this plant, one of which was labeled *S. morrisonii* subsp. *elatus*. The herbarium specimens indicated

to him that the plant was also to be found north of Three Peaks, near Middletown.

Dolan and LaPrè collected several species of *Streptanthus* in the vicinity of Three Peaks for their biochemical genetic studies of the *S. morrisonii* complex (Dolan and LaPrè 1989). They referred to Neilson's report of the undescribed plant in their unpublished consultants' report (Dolan and LePrè 1987). They speculated that it might be related to *Streptanthus batrachopus* J. Morrison, known, then and still, from only two sites in Marin County, but they did not develop the speculation further. In the mid-1980s, Steve Edwards and Chris Thayer also observed a small, yellow-flowered jewelflower near Three Peaks that they believed was related to *S. brachiatus* Hoffman (Edwards personal communication).

As shown above, different observers of the undescribed jewelflower in the area adjacent to Three Peaks came to different conclusions about its relationship to other *Streptanthus* species, but all recognized it as unique. Their observations warrant examination. Table 1 compares the morphological attributes of the new species with those of the three others, plus *S. breweri* var. *hesperidis* Jepson.

The comparisons show that all of the species share some characters but that the new species shares few characters with any single one of them. *S. vernalis* has a unique combination of morphological traits. While *S. breweri* var. *hesperidis* resembles *S. vernalis* in stature, branching habit and second inflorescence, its zig-zag stem, overall yellow color (especially its leaves), greenish-yellow calyx, more connivent sepals and later flowering period set it apart from *S. vernalis*. Although similar in size and habit, other morphological attributes separate *S. batrachopus* from *S. vernalis*. In addition, like *S. breweri* var. *hesperidis*, *S. batrachopus* flowers later than *S. vernalis*. Furthermore, the only known colonies of *S. batrachopus* are separated from *S. vernalis* by about 160 km.

Streptanthus vernalis appears, based on morphological features, to be most similar to *S. morrisonii* subsp. *elatus*. They resemble each other in sepal and petal color, and some basal leaf attributes. They also often have a second inflorescence, arranged in a spiral around the main stem; a feature they share with *S. breweri* var. *hesperidis*. On the other hand, *S. morrisonii* subsp. *elatus* is biennial while *S. vernalis* is annual. In addition, the shape of the basal leaves of *S. morrisonii* in its flowering year resemble those of the annual *S. vernalis* initially, but as *S. morrisonii* grows, its basal leaves become longer, wider, and spatulate. They are also mottled purple/brown adaxially. These leaf features are not seen in *S. vernalis*. In addition, the plants exhibit substantial differences in height, habit, and flowering period.

Streptanthus morrisonii and *Streptanthus vernalis* also differ in vestiture of their calyces. *Streptanthus morrisonii* is comprised of three subspecies,

all of which are tall and branched from about the top third of the main stem, not also from the base as in *S. vernalis*. The calyces of *S. morrisonii* vary from glabrous to villous. The calyces of *S. morrisonii* subsp. *elatus* alone vary with respect to vestiture. At Three Peaks the calyces of *S. morrisonii* subsp. *elatus* that we have observed are glabrous (although Nielson found specimens at Three Peaks that were visibly hispidulous), while less than a mile to the east, in an area Nielson is unlikely to have visited due to the extremely difficult terrain, the calyces of the subspecies are usually hispidulous. The calyces of *S. morrisonii* subsp. *elatus* in Butts Canyon are vested with sparse but longer hairs. (Buds from each of these variants of *S. morrisonii* subsp. *elatus* were used in the allozyme analysis.) In contrast, the calyces of *S. vernalis* are uniformly glabrous.

Abaxially the basal leaves in all of the species discussed herein are more or less purple. Most of the species we have compared to *S. vernalis* also have purple/brown mottling on the upper surfaces of their basal leaves, while *S. vernalis* has no mottling.

The tips of the basal leaf teeth and the tips of the cauline leaves are orange in *S. vernalis* as they are in *S. morrisonii* subsp. *elatus*. These may have the same function as the non-green callosities on the marginal teeth of *S. glandulosus* Hooker, which are believed to function as pierid butterfly egg mimics to deter butterfly ovipositing and subsequent predation (Shapiro 1981).

The flowering periods of the jewelflowers compared to *S. vernalis* herein begin after *S. vernalis* has begun to set seed, with little or no overlap. Differences in seasonal flowering period, even as small as 2 weeks, can contribute significantly to the reproductive isolation of a species (Levin 1971). The early flowering period of *S. vernalis* is probably an effective barrier to gene exchange with any of its neighbors. In addition, *S. morrisonii* subsp. *elatus* and *S. vernalis* may be facultatively autogamous, a condition that increases the probability that they do not exchange genes. Some degree of autogamy is indicated by the enclosure of the two pairs of fertile stamens within the calyx, supertending the short post-like stigma. Dissection of the flower reveals that the stigma is virtually buried in pollen that rains down upon it from the four anthers immediately above it. At one time, the pair of vestigial infertile anthers well exerted from the calyx possibly functioned as agents of pollen dispersal; the atrophy of these organs may indicate selection for facultative self-pollination. The genus contains other autogamous species: *S. batrachopus* and *S. niger* E. Greene (Kruckeberg 1957, 1984).

ALLOZYME ANALYSIS

Morphology, as is often the case, is not the last word in species delimitation. Genetic data for mem-

TABLE 1. MORPHOLOGICAL COMPARISON OF FIVE *STREPTANTHUS* SPECIES. Data are from Hickman (1993), Hoffman (1952), and Personal Observations of *Streptanthus vernalis* over three seasons.

| Attributes | <i>S. vernalis</i> | <i>S. morrisonii</i> subsp. <i>elatus</i> | <i>S. breweri</i> var. <i>hesperidis</i> | <i>S. batrachopus</i> | <i>S. brachiatus</i> |
|------------------|--|--|--|--|---|
| Flowering period | Annual, March–May | Biennial, May–July | Annual, May–July | Annual, May–July | Biennial, May–June |
| Plant height | 2–20 cm | Up to 12 dm | Less than 4 dm | 5–18 cm | 2–6 dm |
| Habit | Usually simple, or ranched from below | Remotely branched | Simple or branched below | Simple or branched from base | Generally branched below |
| Inflorescence | Racemose, sometimes secund | Racemose, often secund | Racemose, often secund, zig-zag | Racemose, lax | Discretely racemose, bracteate or not |
| Leaf, basal | Orbicular, apically crenate, green above, purple below, apical teeth orange-tipped, succulent, 3–4 cm, petiole 1 mm | Purple-mottled above, purple below, oblanceolate, thick, toothed above middle, 3–5 cm long | Entire to coarsely dentate, obovate, less than 5 cm long | Purple-mottled above, obovate, lobed, petioled 1–2.5 cm long | Oblanceolate, toothed above middle, thick, 1.5–4 cm, purple below, mottled-purple/brown above |
| Leaf, cauline | Narrowly lanceolate, entire, sessile, orange-tipped | Narrowly lanceolate, entire, sessile, clasping | Lower clasping, upper generally lanceolate, entire | Sessile, auriculate clasping, linear-lanceolate, entire | Sessile, narrowly ovate, serrate, upper lanceolate |
| Pediceal length | 1–2 mm | Short | Short, if any | 2–3 mm | 1 mm |
| Calyx | Biradial, glabrous | Biradial, glabrous or hispidulous | Biradial, glabrous | Biradial, glabrous, strongly narrowed at tip | Biradial, glabrous |
| Sepal | 6–7 mm, green, yellow toward tips | Up to 7 mm, yellowish | 4–7 mm, greenish yellow | 4 mm, green or purple, white recurved, glabrous tips | Yellow to light purple, 6–9 mm |
| Petal | White, strongly reflexed, 2 mm | White, lightly veined with purple, 9 mm, undulate margins | 6–8 mm, whitish or purple-veined | White with purple mid-vein, 6–7 mm | Upper white or purple veined, lower light purple, 7–9 mm |
| Stamens | Three pairs, upper pair broadly connate, exserted, recurved, middle, inserted, fused to middle, bottom pair free, inserted | Three pairs, upper pair broadly connate, exserted, recurved, middle and lower pairs inserted | Three pairs, upper pair broadly connate, exserted, recurved, middle and lower pairs inserted | Three pairs, upper pair broadly connate, exserted, recurved, middle and lower pairs inserted | Three pairs, upper pair broadly connate, exserted, recurved, middle pair fused at base, lower pair free |
| Silique | Erect, up to 4–5 cm, torulose | Erect to spreading, up to 7.5 cm, torulose | Ascending or spreading, 2–11 cm, curved, narrowed between seeds | Arcuate spreading, 2.5–3 cm | Ascending, narrowed between seeds, 5–7 cm |
| Seed | Orange, winged | Winged at the end | Not winged | Brown, winged | Wing weak |

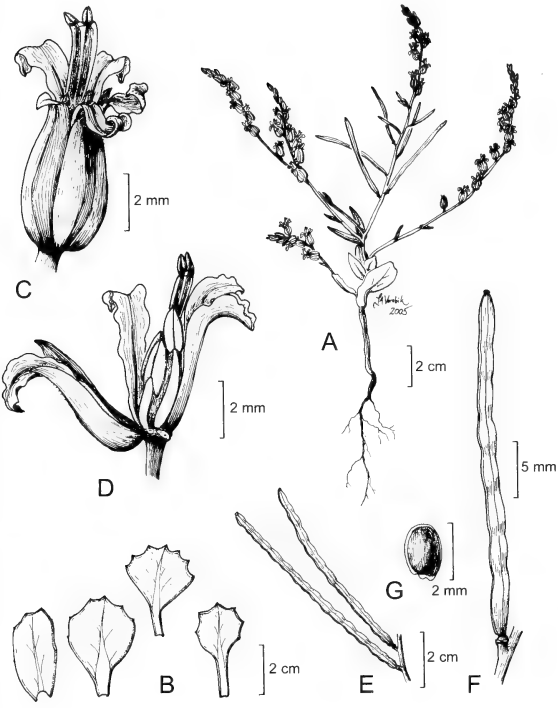


FIG. 1. *Streptanthus vernalis*. A. Habit; B. Leaf variations; C. Flower dissected open; D. Flower dissected open; E. Fruits; F. Fruit; G. Seed.

bers of the *Streptanthus morrisonii* complex has been shown to be incongruent with morphological data (Dolan 1995). Consequently, we conducted allozyme analysis of *S. vernalis* to test its genetic relationship to the species we compared morphologically.

Fresh buds of *S. vernalis* and suspected related species were assayed for allozymes following the procedures of Dolan (1995). With the exception of *Streptanthus batrachopus* buds, which were collected from San Geronimo Ridge in Marin County, the buds used in the analysis were collected from populations within 5 miles of Three Peaks. Data were analyzed using GDA (Lewis and Zaykin 2001).

Clear, repeatedly resolvable bands were obtained from 8–14 individuals per taxa for alcohol dehydrogenase (ADH), phosphoglucoseisomerase (PGI) and Esterase (EST). Fifteen apparent alleles were detected. All taxa had banding patterns consistent with diploidy. *Streptanthus vernalis* exhibited a second EST locus not detected in the other taxa. *Streptanthus breweri* var. *breweri* A. Gray and *S. batrachopus* had an apparent duplicated PGI locus. Absence of these loci in other taxa was scored as an identical character state, indicated by use of a single absent allele designation.

Allozymes revealed *S. vernalis* is genetically distinct from related taxa (Fig. 2). Although only a small number of plants were sampled, the analysis

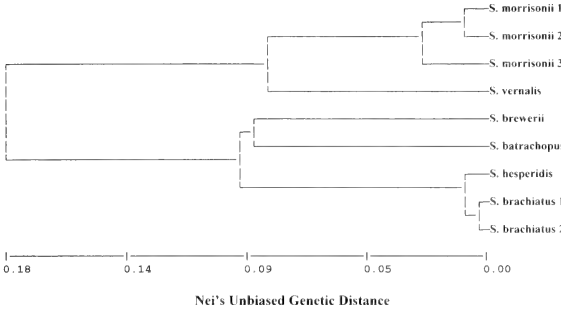


FIG. 2. Cluster diagram of genetic distance between *Streptanthus vernalis* and related taxa based on allozymes. *S. morrisonii* subsp. *elatus* was sampled from 3 different sites, *S. brachiatus* from 2.

clearly indicates that *S. vernalis* is not *S. batrachopus* or *S. brachiatus*, and appears to be most closely allied with *S. morrisonii*.

Cluster analysis (based on Nei's [1978] unbiased genetic distance values clustered by the UPGMA method of Sneath and Sokol [1973]) yielded two distinct branches, placing *S. vernalis* with *S. morrisonii* subsp. *elatus*. *Streptanthus brachiatus* and *S. breweri* var. *hesperidis* cluster closely in a second branch that also shows a close genetic relationship between *S. breweri* var. *breweri* and *S. batrachopus*.

IMPLICATIONS FOR *STREPTANTHUS* TAXONOMY

Streptanthus vernalis has a unique combination of traits. Its four white petals, the lower pair delicately tinted light yellow in the midvein area, do not exhibit the pronounced color dimorphism of *S. breweri* and *S. morrisonii*, the lower petals of which are typically and clearly purplish or brownish. In addition, *S. vernalis* is an annual, the evidence for which is that no resting rosettes among the flowering population have been observed for four seasons of close monitoring. Its annual life form, typical of section *Hesperides*, distinguishes *S. vernalis* from *S. morrisonii* *elatus*, a biennial as are the other members of the section *Biennes*. The allozyme evidence and the morphology of *S. vernalis* indicate a close relationship with *S. morrisonii*. Thus, *S. vernalis* appears to confound the previously recognized boundaries between the section *Biennes* and *Hesperides*. The sectional assignment of *S. vernalis*, if not the entire taxonomy of both sections, warrants further study.

CONCLUSION

Evidence from comparative morphology and genetic analysis indicate that *S. vernalis* is a new species of *Streptanthus*. It is likely related to the *S. morrisonii* complex.

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MEIOTIC AND MITOTIC CHROMOSOME NUMBERS FOR *MENTZELIA LEUCOPHYLLA* BRANDEGEE (LOASACEAE)

WILLIAM S. DAVIS

1424 Hawkshead Lane, Louisville, KY 40220
yelnatsw@bellsouth.net

ABSTRACT

Meiotic and mitotic chromosome numbers for *Mentzelia leucophylla* Brandege (Loasaceae) are reported. The numbers of $n = 11$ and $2n=22$ fit with the aneuploid series that exists in other taxa of *Mentzelia* section *Bartonia*, but differ from a chromosome number of $n = 18$ reported in 1973 by Reveal & Styer. Although additional work should be done on the species, it is suggested that the 1973 count may be in error.

Key Words: Loasaceae section *Bartonia*, *Mentzelia leucophylla*, meiotic chromosome numbers, mitotic chromosome numbers.

A recent report of a new species of *Mentzelia* (Thompson and Prigge 2004) also lists chromosome numbers and morphological characteristics of other species in section *Bartonia* (Loasaceae) from California and Nevada. It is clear from Table 1 of that paper that the reported chromosome number of $n = 18$ for *M. leucophylla* (Reveal & Styer 1973) does not fit with the aneuploid series that exists in section *Bartonia*. In a footnote in Table 1, it is stated that this count needs to be checked. As a matter of fact, relevant chromosome counts of this species have been made, but not published. These counts were inadvertently omitted from Table 1. In 1969, at the University of California, Los Angeles, meiotic counts of $n = 11$ were obtained from *M. leucophylla* by H. J. Thompson. The plants analyzed were grown from seeds taken from a herbarium specimen (Reveal 1484, 0.4 mi nw of Ash Meadows Road on road to Crystal Pool, 4 Jul 1968, Nye

County, Nevada). In addition, in 1987, at the University of Louisville, I germinated seeds collected from six plants of *M. leucophylla* at the type locality in Ash Meadows. I observed mitotic chromosome numbers of $2n=22$ in root tip cells of each plant, confirming the unpublished counts of H. J. Thompson. Although additional work should be done on the species, these data suggest that the original count of $n = 18$ for *M. leucophylla*, may be in error.

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NOTEWORTHY COLLECTIONS

CALIFORNIA

PENSTEMON PAHUTENSIS N. Holmgren (SCROPHULARIACEAE).—Inyo Co., Grapevine Mountains, Death Valley National Park, UTM Zone 11 487661E 4088993N (NAD 83), in pinyon-juniper woodland at wash bottom, 13 June 2001, Brian Knaus 14 (RSA); Inyo Co., Grapevine Mountains, Death Valley National Park, UTM Zone 11 487873E 4089066N (NAD83), in pinyon-juniper woodland at wash bottom, 13 June 2001, Brian Knaus 15 (DEVA). Associated with *Pinus monophylla*, *Artemisia tridentata* ssp. *vaseyana*, *Chrysothamnus viscidiflorus* ssp. *viscidiflorus*, *Ephedra viridis*, *Purshia tridentata* var. *glandulosa*, *Achnatherum hymenoides*, *Cryptantha flavoculata*, and *Phacelia tanacetifolia*.

Previous knowledge. This species was originally described in 1971 as occurring commonly at Pahute Mesa and Rainier Mesa in south-central Nye County, NV (N. H. Holmgren 1971, Aliso 7:351–356). The Jepson Manual (Hickman 1993) indicates that *P. pahutensis* also occurs in the Grapevine Mountains, a range located in eastern

Inyo County, California, and western Nye county, Nevada (the state line bifurcates the range near its crest). It is notable that the “Von Schmidt Line,” a historical state boundary, lies easterly and parallel to the current state boundary in this region. The Grapevine Mountains are currently contained within Death Valley National Park.

On June 9, 1891, F.V. Coville and F. Funston 1759 (NY, digital image!) collected “*Penstemon glaber* Pursh.” at “Wood Cañon, Grapevine Mountains, California.” Noel Holmgren subsequently annotated this specimen as *P. pahutensis*. To this author’s knowledge there is currently no canyon in the Grapevine Mountains known as “Wood Canyon.” Coville’s account (1893, Contributions from the U. S. National Herbarium 4) states that Mr. Funston was engaged in a trip across Death Valley to Grapevine Peak, and back to Keeler, CA during the period May 23 to June 15. (From May 24 to June 10, Coville stayed in Keeler.) Although Coville states that Mr. Funston returned by the same route (1893, Contributions from the U. S. National Herbarium 4: 7), the map in this volume

includes two paths from Death Valley to the ridgeline of the Grapevine Mountains. Both of these routes are north of Boundary Canyon, where Nevada State Highway 374 currently traverses the Grapevine Mountains. Perhaps these two routes included Titus Canyon and Fall Canyon, but no place names are given. On June 12, 1891, *Pinus flexilis* James was collected at the summit of the peak of Grapevine Mountain (Coville & Funston 1767), suggesting that the *Penstemon* collection was made during the ascent towards the ridge from the California side, or along the ridge in Nevada. This collection may represent the first collection of *P. pahutensis* in California but the location of this collection is ambiguous due to its close proximity to the California/Nevada boundary and the lack of detail in Coville's report.

On June 23, 1935, *M. F. Gilman* 1804 (NY, digital image!) collected "*Penstemon speciosus* Dougl." at "Inyo County: Head of Titus Canyon, Grapevine Mts., Death Valley, at 2135 m (7000 ft) elevation." Noel Holmgren also annotated this specimen as *P. pahutensis*. While Titus Canyon is currently a popular tourist destination in Death Valley National Park, it is uncertain whether this site was indeed inside California. The elevation suggests that the collection occurred just outside California in Nye County, Nevada. *Gilman* 3213 (DEVA) also collected *Penstemon speciosus* from Grapevine Mine at 6500 feet elevation (Dana York, Death Valley National Park Botanist, personal communication). Grapevine Mine is located on the Nevada side of the Grapevine Mountains. I have not seen this specimen and it is unknown whether it should also be annotated to *P. pahutensis*.

Additional collections (*G. E. Lyon*, 217, 218, 234, 235, 236, 237, DEVA!) were made in 1994 from the Grapevine Mountains as part of a study questioning the validity of this species. These collections were labeled as having been collected from Inyo County, CA. However, the site descriptions, UTM coordinates, and the maps that were submitted with the collections (assumedly provided by G. E. Lyon and available at the Death Valley National Park Museum Library) clearly show them to have been collected from Nye County, NV.

Significance. These collections confirm the occurrence of *Penstemon pahutensis* in the State of California. Several historical specimens suggested its presence within the state but the exact location of their collection is ambiguous. While there have previously been collections in Nye County, NV and the distribution could have been expected to extend into California, there was no validation. The remote location and lack of roads to this area have thus far prevented confirmation. Though it was recently removed from the California Native Plant Society's Inventory of Rare and Endangered Plants (sixth edition, 2001) due to lack of evidence for its occurrence in the state, this collection of *Penstemon pahutensis* indicates it should be included in the next edition.

This collection emphasizes the lack of botanical information we possess for the California–Nevada desert regions. These areas are rich in local endemics due to many factors including their diverse topographic, hydrologic and

edaphic features. Recent collections have highlighted the fact that even common species (Pritchett *et al.* 2001, Madroño 48: 43) have gone undetected until very recently. The largest risk to these desert communities are land management decisions, such as the nearby Yucca Mountain nuclear waste storage facility, being made on a paucity of information for the region. This lack of information is frequently based not on lack of knowledge (existing in the literature as well as in herbaria), but results from the lack of botanists going out there to look and confirm, as I believe this collection illustrates.

—BRIAN J. KNAUS, Department of Botany and Plant Pathology, Oregon State University, 2082 Cordley Hall, Corvallis, OR 97331-2902. Knausb@science.oregonstate.edu.

CALIFORNIA

COTONEASTER SIMONSII Baker (ROSACEAE).—Del Norte Co., adventive in thickets, Route 199, Hiouchi, elev. 40 m, 18 May 2004, *P. F. Zika* 19638 (UC, WTU); spread from cultivation to thickets, near airport, Gasquet, elev. 40 m, 18 May 2004, *P. F. Zika* 19639 (UC, WTU).

Previous knowledge. Native to the Himalayas, Himalayan cotoneaster is a occasional escape from cultivation on the coast of Oregon and Washington. It is a winter deciduous shrub, and thus easily distinguished from the other three naturalized species in California, which are evergreen (Hrusa *et al.* 2002, Madroño 49: 61–98; Rosatti, T. J. 1993, *Cotoneaster*, In: The Jepson Manual Higher Plants of California, University of California Press, Berkeley, CA). A key to wild members of the genus in California is provided below. These ornamentals are popular for their bright fruits that persist in autumn and winter. The seeds are dispersed by frugivorous birds such as American robins (*Turdus migratorius*) and cedar waxwings (*Bombicilla cedrorum*).

1. Leaves deciduous, lower surface green and sparsely pubescent; anthers cream *C. simonsii*
1. Leaves evergreen, lower surface obscured, densely tomentose; anthers pink
 2. Flowers cupulate, petals pink and erect; styles 2–4, always some flowers with more than 2 styles; always some fruits with more than 2 stones *C. franchetii* Bois
 2. Flowers rotate, petals pure white, spreading; styles 2; fruits with 2 stones
 3. Leaves thin and flat, veins superficial; leaves 10–30 × 10–20 mm wide *C. pannosus* Franch.
 3. Leaves thick, slightly wrinkled with sunken veins; leaves 30–95 × 17–45 mm wide *C. lacteus* W. W. Sm.

Significance. First report as a wild plant in California.

—PETER F. ZIKA, Herbarium, Burke Museum, Box 355325, University of Washington, Seattle, WA 98195–5325.

WASHINGTON

AESCULUS HIPPOCASTANUM L. (HIPPOCASTANACEAE).—King Co., Jensens Cove, Lake Sammamish, elev. 8 m, 7 Oct 1999, *P. F. Zika 14561*, Weinmann & Jacobson (WTU); 0.8 km S of Rattlesnake Lake, elev. 300 m, 18 Sep 2001, *Zika 16567* (WTU); spontaneous in rocky, Montlake, Seattle, elev. 30 m, 5 Apr 2000, *Zika 14903* (WTU); fruiting, 100 m from cultivated trees, N end of Mercer Island, Lake Washington, elev. 15 m, 10 Nov 2004, *Zika 20431* (WTU); Pierce Co., Snake Lake, Tacoma, elev. 110 m, 22 Mar 2004, *Zika 19300* (WTU); San Juan Co., garden weed, Roche Harbor, San Juan Island, elev. 6 m, 13 Oct 2000, *Zika 15567* (WTU).

Previous knowledge. Horse chestnut is native to Europe, and spread from cultivation to disturbed woodlots in western Oregon.

Significance. First collections as an escape from cultivation in Washington.

AMELANCHIER LAEVIS Wiegand (ROSACEAE).—King Co., willow thickets, Union Bay, Lake Washington, Seattle, elev. 4 m, 3 Apr 2003, *P. F. Zika 18187* (WTU); same site, 29 Mar 2004, *Zika 19337* (WTU).

Previous knowledge. Smooth serviceberry is native to eastern North America, west to Minnesota.

Significance. First collection as an escape from cultivation in Washington.

ARBUTUS UNEDO L. (ERICACEAE).—King Co., campus of University of Washington, Seattle, elev. 25 m, 7 Nov 1999, *P. F. Zika 14710* (OSC, WTU); same site, 9 Nov 2004, *Zika 20429* (NY, UBC, UC, WTU); steep blackberry slope, N Northlake Way, Seattle, elev. 10 m, 22 Nov 2004, *Zika 20443* (WTU).

Previous knowledge. Strawberry tree is native to Europe.

Significance. First collections as an escape from cultivation in Washington.

AUCUBA JAPONICA Thunb. (CORNACEAE).—King Co., open woods, garden dump, near shore of Portage Bay, Lake Union, Seattle, elev. 5 m, 17 Apr 2001, *P. F. Zika 15892* (WTU); brushy hillside, S end of Washington Park arboretum, Seattle, elev. 30 m, 30 Jan 2003, *Zika 18159* (WTU); thickets near small creek, arboretum, Seattle, elev. 20 m, 11 Nov 2004, *Zika 20435* (WTU).

Previous knowledge. Spotted laurel is native to Japan.

Significance. First collections as escapes from cultivation in Washington.

BERBERIS THUNBERGII DC. (BERBERIDACEAE).—King Co., Union Bay, Lake Washington, Seattle, elev. 4 m, 25 Apr 2001, *P. F. Zika 15968* (WTU); Whitman Co., South Fork Palouse River, Pullman, elev. 710 m, 30 May 2004, *Zika 19718* & *R. Old* (WS, WTU).

Previous knowledge. Japanese barberry is native to Japan.

Significance. First collections as escapes from cultivation in Washington.

CAMPANULA POSCHARSKYANA Degen (CAMPANULACEAE).—King Co., campus of University of Washington, Seattle, elev. 25 m, 7 Jun 2000, *P. F. Zika 15100d* (WTU); cracks in concrete wall, Montlake, Seattle, elev. 25 m, 25 May 2000, *Zika 15016* & *A. L. Jacobson* (WTU); cracks in walls and concrete sidewalks, Green Lake, Seattle, elev. 50 m, 24 July 2001, *Zika 16402* & *Jacobson* (WTU).

Previous knowledge. Trailing bellflower is an ornamental native to Jugoslavia.

Significance. First collections as escapes from cultivation in Washington.

CONYZA BONARIENSIS (L.) Cronquist (ASTERACEAE).—King Co., gravel parking, campus of University of Washington, Seattle, elev. 10 m, Sep 1999, *A. L. Jacobson s.n.* (WTU); cracks in asphalt near Seahawk Stadium, Occidental Avenue, Seattle, elev. 7 m, 13 Jan 2003, *P. F. Zika 18157* & *Jacobson* (WTU).

Previous knowledge. Argentine fleabane is native to South America, and a weed in British Columbia and Oregon.

Significance. First collections for Washington.

CORNUS SANGUINEA L. (CORNACEAE).—King Co., Lakeview Park, Harrison Ridge, Seattle, elev. 50 m, 14 Oct 1999, *P. F. Zika 14587* & *A. L. Jacobson* (WTU); campus of University of Washington, Seattle, elev. 25 m, 26 Oct 1999, *Zika 14656* & *Jacobson* (WTU); thickets, Washington Park arboretum, Seattle, elev. 25 m, 17 Nov 1999, *Zika 14735* & *Jacobson* (WTU).

Previous knowledge. European dogwood is native to Europe.

Significance. First collections as escapes from cultivation in Washington.

CORTADERIA JUBATA (Lemoine ex Carrière) Stapf (POACEAE).—King Co., waste ground near Interstate 5, Seattle, elev. 45 m, 1 Nov 2001, *P. F. Zika 16721* & *A. L. Jacobson* (NMCR, WTU, dupl. det. by Kelly Allred); Snohomish Co., gravel ditch, Alderwood Manor, elev. 150 m, 12 Oct 2000, *Zika 15565* (WTU).

Previous knowledge. Purple pampas grass is native to South America and invasive on the coast of California and Oregon. The Flora of North America maps *Cortaderia jubata* in Washington state, based on these vouchers (Allred 2003, *Cortaderia*, In: Flora of North America North of Mexico; Volume 25 Magnoliophyta: Commelinidae (in part): Poaceae, part 2. Oxford University Press, New York).

Significance. First collections as escapes from cultivation in Washington.

CORTADERIA SELLOANA (Schult. & Schult. f.) Asch. & Graebn. (POACEAE).—King Co., adventive among boulders, Van Asselt, Seattle, elev. 50 m, 30 Oct 2000, *P. F. Zika 15618* (WTU); Snohomish Co., dry disturbed ground, near Snohomish River, Everett, elev. 15 m, 18 Sep 2002, *Zika 17876* & *F. Weinmann* (NMCR, WTU).

Previous knowledge. Pampas grass is native to South America and invasive on the coast of California. The Flora of North America maps *Cortaderia selloana* in Washington state, based on these vouchers (Allred 2003, *Cortaderia*, In: Flora of North America North of Mexico; Volume 25 Magnoliophyta: Commelinidae (in part): Poaceae, part 2. Oxford University Press, New York).

Significance. First collections as escapes from cultivation in Washington.

ELAEAGNUS UMBELLATA Thunb. (ELAEAGNACEAE).—King Co., brushy fields, Sand Point, Lake Washington, Seattle, elev. 10 m, 17 May 2002, *P. F. Zika 16889* & *A. L. Jacobson* (WTU).

Previous knowledge. Spreading oleaster is native to eastern Asia, and sparingly naturalized in northwest Oregon.

Significance. First collection as a garden escape in Washington.

ERIGERON KARVINSKIANUS DC. (ASTERACEAE).—King Co., cracks in brickwork, Pioneer Square, Seattle, elev. 5 m, 12 Dec 2001, *P. F. Zika 16732* & *A. L. Jacobson* (WTU); crack in concrete bridge, Madison Park, Seattle, elev. 30 m, 30 Sep 2002, *Zika 17983* (WTU); cracks in

concrete driveway, Montlake, Seattle, elev. 25 m, 8 Nov 2002, *Zika 18150* (WTU); occasional escape near Loyal Heights Playfield, Ballard, Seattle, elev. 70 m, 21 Sep 2003, *Zika 19089* & *Jacobson* (WTU).

Previous knowledge. Mexican fleabane is native to Mexico and adventive in California.

Significance. First collections as garden escapes in Washington.

EUPHORBIA SERRULATA Thuill. (EUPHORBIACEAE).—King Co., near stadium, campus of University of Washington, Seattle, elev. 10 m, 27 Jun 2000, *A. L. Jacobson s.n.* (WTU); Allen Library, campus of University of Washington, Seattle, elev. 30 m, 20 Jun 2001, *P. F. Zika 16314* & *Jacobson* (WTU); Fremont, Seattle, elev. 7 m, 22 July 2001, *Zika 16387* (WTU).

Previous knowledge. Upright spurge is annual and native to Europe.

Significance. First collections for Washington.

HEDERA HIBERNICA (G. Kirchn.) Bean (ARALIACEAE).—Clallam Co., creekbank, Port Angeles, elev. 35 m, 3 Jun 2004, *P. F. Zika 17999* (WTU); Clark Co., Burnt Bridge Creek, Vancouver, elev. 15 m, 29 Apr 2004, *Zika 19456* (WTU); Cowlitz Co., Lewis River, 4 air km SSE of Woodland, elev. 10 m, 12 Mar 2004, *Zika 19285* (WTU); Island Co., Oak Harbor, Whidbey Island, elev. 10 m, 4 Jun 2004, *Zika 19813* (WTU); King Co., Lake City, elev. 10 m, 11 Jan 2000, *Zika 14793* (WTU); Kitsap Co., University of Washington Big Beef Research Facility, elev. 6 m, 3 May 2003, *D. Giblin 3–36* & *B. Legler* (WTU); Lewis Co., Pe Ell Prairie, E side of Chehalis River, elev. 110 m, 13 May 2004, *Zika 19549* (WTU); Pacific Co., NE of Chinook Point, elev. 50 m, 13 May 2004, *Zika 19557* & *C. L. Maxwell* (WTU); Pierce Co., Snake Lake, Tacoma, elev. 100 m, 22 Mar 2004, *Zika 19294* (WTU); San Juan Co., common escape near ferry landing, Friday Harbor, 7 May 1992, *S. R. Atkinson 387* (WTU); Skagit Co., Grandy Creek, Birdsview Siding, elev. 55 m, 26 Apr 2004, *Zika 19441* (WTU); Snohomish Co., Deer Creek, Woodway, elev. 80 m, 27 Mar 2004, *Zika 19332* (WTU); Thurston Co., Frye Cove Park, 15 May 2000, *E. B. Walling 49* (herbarium of The Evergreen State College); Pacific Co., Cases Pond, Raymond, elev. 7 m, 13 May 2004, *Zika 19552* (WTU); Whatcom Co., Lake Terrill Wildlife Area, W of Ferndale, elev. 46 m, 19 Apr 2003, *B. Legler 222* (WTU); Sehome Hill, Bellingham, elev. 100 m, 5 Jun 2004, *Zika 19820* (WTU).

Previous knowledge. Atlantic ivy is native to Europe, and a greater pest in natural areas than English ivy, *Hedera helix* L. (*A. L. Jacobson 2001, Wild Plants of Greater Seattle*, publ. by the author, Seattle, WA). Two Seattle collections from 1889–1890 (*Shumway 4158, Burplehaus 4158* WTU) are not labeled as either ornamental or wild plants. We treat those early collections as cultivated, following Piper (1906, *Flora of the State of Washington*. Contributions from the U. S. National Herbarium, Volume 11. Government Printing Office, Washington, D. C.), and they indicate the species has a long garden history in the area.

Significance. First collections as garden escapes in Washington.

ILEX CRENATA Thunb. (AQUIFOLIACEAE).—Snohomish Co., Scriber Lake Park, Lynnwood, elev. 100 m, 21 Oct 2004, *P. F. Zika 20423* & *A. L. Jacobson* (WTU).

Previous knowledge. Japanese holly, native to eastern Asia, is naturalized in the eastern United States.

Significance. First collection as a garden escape in Washington.

IRIS FOETIDISSIMA L. (IRIDACEAE).—King Co., Chit-

tenden Locks, Seattle, elev. 10 m, 20 Mar 2000, *P. F. Zika 14854* & *A. L. Jacobson* (WTU); Foster Island, Lake Washington, Seattle, elev. 5 m, 6 Jan 2001, *Zika 15748* (WTU); NE shore, Union Bay, Lake Washington, Seattle, elev. 5 m, *Zika 16308* (WTU).

Previous knowledge. Stinking iris is native to Europe, and naturalized in California (Hrusa et al. 2002, Madroño 49: 61–98).

Significance. First collections as garden escapes in Washington.

LIGUSTRUM OBTUSIFOLIUM Siebold & Zucc. (OLEACEAE).—King Co., Ravenna Park, Seattle, elev. 50 m, 13 Jun 2004, *P. F. Zika 19840* (WTU); same site, 20 Nov 2004, *Zika 20442* (WTU).

Previous knowledge. Border privet is native to Asia, and adventive in the eastern United States.

Significance. First collection as a garden escape in Washington.

LIGUSTRUM OVALIFOLIUM Hassk. (OLEACEAE).—King Co., near Route 520, Montlake, Seattle, elev. 15 m, 15 Jun 2004, *P. F. Zika 19858* (OSC, UBC, UC, WTU).

Previous knowledge. California privet is native to Japan, and naturalized in California (Hrusa et al. 2002, Madroño 49: 61–98).

Significance. First collection as a garden escape in Washington.

LIGUSTRUM VULGARE L. (OLEACEAE).—Clark Co., escaped at Vancouver, 1 Jun 1926, *J. W. Thompson s.n.* (WTU); King Co., Sand Point, Lake Washington, elev. 10 m, 30 Sep 2002, *P. F. Zika 17996* & *A. L. Jacobson* (WTU); same site, 14 Jun 2004, *Zika 19846* (WTU); Pierce Co., Snake Lake, Tacoma, elev. 100 m, 22 Mar 2004, *Zika 19307* (WTU); Thurston Co., Scatter Creek, Scatter Creek Wildlife Area, elev. 60 m, 15 Oct 2001, *Zika 16690* & *F. Weinmann* (WTU); same site, 7 Jun 2004, *Zika 19834* (WTU); Moxlie Creek, Olympia, elev. 20 m, 25 Mar 2004, *Zika 19316* (WTU).

Previous knowledge. Common privet is native to Europe, and naturalized in much of temperate North America, including Oregon and British Columbia.

Significance. First collections as garden escapes in Washington.

LONICERA × BELLA Zabel (CAPRIFOLIACEAE).—King Co., undeveloped property, with other invasives, Snohomish Co. line, 3 May 1998, *C. S. Isler 31–5–98* (WTU); Whitman Co., South Fork Palouse River, Pullman, elev. 710 m, 30 May 2004, *P. F. Zika 19719* & *R. Old* (WS, WTU).

Previous knowledge. Hybrid honeysuckle is the product of *L. morrowi* A. Gray × *L. tatarica* L. In northeastern North America it commonly escapes and is an aggressive weed.

Significance. First collections as garden escapes in Washington.

LONICERA JAPONICA Thunb. ex Murray (CAPRIFOLIACEAE).—Asotin Co., thickets, 1.5 miles E of Silcott, elev. 220 m, 1 Oct 2001, *P. F. Zika 16661* (WTU); King Co., spread from cultivation, shoreline thickets, Mercer Island, Lake Washington, elev. 5 m, 6 Oct 1999, *Zika 14525* & *F. Weinmann* (WTU); same site, 12 Dec 2000, *Zika 15723* & *A. L. Jacobson* (WTU).

Previous knowledge. Japanese honeysuckle is an Asian species with black fruits. It is planted occasionally as an ornamental in western Washington, but is not seen in gardens or in natural areas as commonly as the red-fruited *Lonicera periclymenum* L. *Lonicera japonica* is an abundant weed in the eastern United States, and is naturalized in California.

Significance. First collections as garden escapes in Washington.

LONICERA TATARICA L. (CAPRIFOLIACEAE).—Whitman Co., palouse prairie remnant, Pullman, elev. 720 m, 30 May 2004, *P. F. Zika 19713* & *R. Old* (WS, WTU).

Previous knowledge. Tatarian honeysuckle is Asian, and an aggressive weed in much of temperate North America.

Significance. First collection as a garden escape in Washington.

LONICERA XYLSTHEUM L. (CAPRIFOLIACEAE).—King Co., adventive on creekbank, Washington Park arboretum, Seattle, elev. 15 m, 23 Apr 2004, *P. F. Zika 19417* (WTU); same site, 8 Jul 2004, *Zika 19883* (WTU).

Previous knowledge. European fly-honeysuckle is native to Europe, naturalized in the northeastern United States, and is reported wild in Oregon.

Significance. First collection as a garden escape in Washington.

MALUS BACCATA (L.) Borkh. var. *BACCATA* (ROSACEAE).—King Co., adventive on margin of mowed fields, near Union Bay, Lake Washington, Seattle, elev. 10 m, 17 May 2002, *Zika 16894* & *A. L. Jacobson* (WTU); same site, 15 Oct 2002, *Zika 18108* (WTU); Yakima Co., E side of Yakima River, between Yakima and Terrace Heights, elev. 320 m, 14 Oct 2002, *Zika 18102* (WTU).

Previous knowledge. Siberian crabapple is native to Asia, and naturalized in northeastern North America. For crabapple identification see the keys in Huckins (1967, Bailey 15: 129–164).

Significance. First collections as garden escapes in Washington.

MALUS HUPEHENSIS (Pamp.) Rehder (ROSACEAE).—King Co., adventive in brushy fields, Sand Point, Lake Washington, Seattle, elev. 10 m, 17 May 2002, *P. F. Zika 16892* & *A. L. Jacobson* (WTU); same site, 30 Sep 2002, *Zika 18008* & *Jacobson* (WTU).

Previous knowledge. Tea crabapple is native to Asia. American robins (*Turdus migratorius*) eat the fruit and disperse the seed.

Significance. First collection as a garden escape in Washington.

MALUS PRUNIFOLIA (Willd.) Borkh. var. *PRUNIFOLIA* (ROSACEAE).—King Co., adventive, mowed field margin, Union Bay, Lake Washington, Seattle, elev. 5 m, 9 Sep 2002, *P. F. Zika 17786* (WTU); brushy fields, Sand Point, Lake Washington, Seattle, elev. 10 m, 30 Sep 2002, *Zika 18002* & *A. L. Jacobson* (WTU); Snohomish Co., disturbed ground by railroad, Edmonds, elev. 5 m, 10 Oct 2001, *Zika 16682* & *Jacobson* (WTU).

Previous knowledge. Chinese or plumleaf crabapple is native to China.

Significance. First collections as garden escapes in Washington.

MALUS SARGENTII Rehder (ROSACEAE).—King Co., uncommon adventive, damp soils, brushy fields, Sand Point, Lake Washington, Seattle, elev. 10 m, 17 May 2002, *P. F. Zika 16891* & *A. L. Jacobson* (WTU); same site, 30 Sep 2002, *Zika 18006* & *Jacobson* (WTU).

Previous knowledge. Sargent crabapple is native to Japan. American robins (*Turdus migratorius*) eat the fruit and disperse the seed.

Significance. First collections as garden escapes in Washington.

PERILLA FRUTESCENS (L.) Britton var. *FRUTESCENS* (LAMIACEAE).—King Co., purple foliage, adventive in cracks in concrete sidewalk and adjacent rubble, Georgetown, Seattle, elev. 70 m, 18 Oct 2004, *P. F. Zika 20422* & *A. L. Jacobson* (WTU).

Previous knowledge. Shiso, or beefsteak plant, is native to eastern Asia, and cultivated as a condiment. It is naturalized in the eastern United States.

Significance. First collection as a garden escape in Washington.

PRUNUS LUSITANICA L. (ROSACEAE).—Grays Harbor Co., Hoquiam River, 6 air km SSE of New London, elev. 10 m, 3 Jun 2004, *P. F. Zika 19793* (WTU); King Co., Washington Park arboretum, Seattle, elev. 20 m, 18 Jun 2001, *Zika 16279* (WTU); Juanita High School, Kirkland, elev. 35 m, 2 Nov 2003, *Zika 19265* (WTU); Kitsap Co., pondshore, Bainbridge Island, elev. 30 m, 17 Nov 1999, *Zika 14725* & *A. L. Jacobson* (WTU); disturbed forest, Bremerton, elev. 30 m, 5 Sep 2001, *Zika 16489* (WTU); Pierce Co., Titlow Beach Park, Tacoma, elev. 20 m, 22 Mar 2004, *Zika 19310* (WTU); San Juan Co., ledges, West Side Road, San Juan Island, elev. 37 m, 1 Apr 2000, *Zika 14898* (WTU); Snohomish Co., 3 miles NW of Lake Ballinger, elev. 50 m, 5 Feb 2000, *Zika 14803* (WTU); Deer Creek, Woodway, elev. 80 m, 27 Mar 2004, *Zika 19327* (WTU); Scriber Lake Park, Lynnwood, elev. 95 m, 25 May 2004, *Zika 19692* (WTU); Thurston Co., Moxlie Creek, Olympia, elev. 20 m, 25 Mar 2004, *Zika 19315* (WTU).

Previous knowledge. Portugal laurel is native to Europe, and naturalized in Oregon and California.

Significance. First collections as garden escapes in Washington.

PRUNUS SEROTINA Ehrh. (ROSACEAE).—King Co., Union Bay, Lake Washington, Seattle, elev. 15 m, 3 Aug 2000, *P. F. Zika 15194* & *A. L. Jacobson* (WTU); Washington Park arboretum, Seattle, elev. 20 m, 26 Oct 2000, *Zika 15589* (WTU); campus of University of Washington, Seattle, elev. 25 m, 26 Oct 1999, *Zika 14672* & *Jacobson* (WTU); same site, 9 Jun 2003, *Zika 18454a* (WTU).

Previous knowledge. Black cherry is native to eastern North America, west to North Dakota and Arizona. It is sparingly naturalized in British Columbia.

Significance. First collections as garden escapes in Washington.

TAXUS BACCATA L. (TAXACEAE).—King Co., Washington Park arboretum, Seattle, elev. 10 m, 15 Sep 1999, *P. F. Zika 14337* & *A. L. Jacobson* (WTU); shoreline, Mercer Island, Lake Washington, elev. 10 m, 6 Oct 1999, *Zika 14527*, *Weinmann* & *Jacobson* (WTU); Lakeview Park, Harrison Ridge, Seattle, elev. 50 m, 14 Oct 1999, *Zika 14582* & *Jacobson* (WTU).

Previous knowledge. English yew is native to Europe, and escapes from gardens in the northeastern United States.

Significance. First wild collections in Washington.

VIBURNUM LANTANA L. (CAPRIFOLIACEAE).—King Co., shoreline, Mercer Island, Lake Washington, elev. 10 m, 6 Jun 2001, *P. F. Zika 16177* & *A. L. Jacobson* (WTU); Skamania Co., Kramer Road 4.8 km from Underwood, 17 May 1975, *S. Ternahan* (ELRG); Yakima Co., wild seedlings and saplings common under planted conifers, arboretum, Yakima, elev. 305 m, *Zika 18089* (WTU).

Previous knowledge. Wayfaring tree is native to Europe, and naturalized in eastern North America and Montana.

Significance. First collections as garden escapes in Washington.

VIBURNUM OPULUS L. var. *OPULUS* (CAPRIFOLIACEAE).—Clark Co., Burnt Bridge Creek, Vancouver, elev. 50 m, 3 Oct 2002, *P. F. Zika 18015* (WTU); King Co., Union Bay, Lake Washington, Seattle, elev. 4 m, 27

Aug 1999, *Zika* 14144 & A. L. Jacobson (WTU); Mercer Slough, Bellevue, elev. 5 m, 6 Oct 1999, *Zika* 14548 & F. Weinmann (WTU); shoreline, Mercer Island, Lake Washington, elev. 5 m, 6 Oct 1999, *Zika* 14534 & Weinmann (WTU); Lake Sammamish, Marymoor Park, elev. 10 m, 7 Oct 1999, *Zika* 14567 & Jacobson (WTU); [Mason, Skamania, or Wahkiakum Co.], Cape Horn, 7 Jun 1904, C. V. Piper 4976 (WTU); Snohomish Co., Lake Roesiger, elev. 180 m, 6 Jun 2004, *Zika* 19826 (WTU); Spokane Co., Little Spokane River, Dartford, elev. 480 m, 31 Aug 2004, *Zika* 20132 (WS, WTU); Whatcom Co., rocky slope, Newhalem, 6 Jun 1991, Naas & Arnot 5624 (WTU).

Previous knowledge. Guelder-rose, or cranberry tree, is an ornamental native to Europe, and adventive in eastern North America and Montana. Reported for Washington by Piper (op. cit.), but dismissed by subsequent authors, after Abrams and Ferris (1960, Illustrated Flora of the Pacific States Washington, Oregon and California: Volume IV, Bignoniaceae to Compositae. Stanford University Press,

Stanford, CA) noted "few localities . . . evidently not established as an introduction."

Significance. Naturalized in Washington.

VIBURNUM TINUS L. (CAPRIFOLIACEAE).—King Co., steep slope 0.5 km N of Point Williams, Seattle, elev. 45 m, 14 Sep 1999, P. F. Zika 14327 (WTU); Washington Park arboretum, Seattle, elev. 6 m, 10 Nov 1999, *Zika* 14714 & A. L. Jacobson (WTU); N end of Mercer Island, Lake Washington, elev. 15 m, 14 Mar 2004, *Zika* 19286 (WTU).

Previous knowledge. Laurustinus is native to Europe, and a local escape from gardens in California (Hrusa et al. 2002, Madroño 49: 61–98).

Significance. First collections as garden escapes in Washington.

—PETER F. ZIKA, Herbarium, Burke Museum, Box 355325, University of Washington, Seattle, WA 98195-5325, Zikap@aol.com; ARTHUR L. JACOBSON, 2215 E. Howe St., Seattle, WA 98112.

REVIEW

Tending Fire: Coping with America's Wildland Fires. By STEPHEN J. PYNE. 2001. Island Press, Washington D.C. 238 pp. \$25.00. ISBN 1-55963-565-7.

In his most recent book, renowned fire historian Stephen J. Pyne departs from his previous efforts that focused primarily on the culture of fire and turns his attention instead towards fire policy. The shift seems to be a bit uncomfortable for Pyne as he utilizes the same writing and research style that helped make so many of his past works, especially his 1995 "World of Fire," such a pleasure to read. Formulating wildfire policy and developing appropriate fire management strategies require a different approach to data verification and interpretation than does delving into cultural history. Consequently, there are sections in the book where literary hyperbole clashes with the need for a more analytical perspective. But Pyne's efforts are ultimately successful because he is able to offer many valuable and compelling viewpoints that need to be seriously discussed by not only the fire community, but scientific and educational institutions as well.

Throughout, Pyne describes a creative and more descriptive way to view fire than most of us have done in the past. It is not just an extreme event on the periphery of biology, but rather an integral part of life. Such a perspective will hopefully stimulate the inclusion of fire in biology texts as not only an important evolutionary force, but also a crucial element of the biotic environment. Pyne's basic premise is that fire needs to be defined primarily as a "phenomenon of the biosphere," because "fire's biological character is fundamental, for without life, fire would not exist." Such an ecological perspective is now being recognized by most land managers as they try to figure out how to safely return fire to landscapes that have been damaged by improper logging and grazing practices as well as overly ambitious fire suppression efforts. But Pyne makes it clear that a one-size-fits-all approach to wildfire management is not appropriate. He states that, "America does not, in truth, have a fire problem or a fire story. It has many fire problems...each of which requires different treatments." This contrasts with a more anthropogenic perspective that views the fire problem not as a fire problem, but as a people problem (Zedler 2005).

As is the case with most books dealing with American wildfires, California ecosystems, especially chaparral, are poorly represented and understood. This is unfortunate because 12 of the nation's top 15 most destructive wildfires have occurred in California. This lack of attention leads one to think fire suppression in southern California over the past

century has led to a steady reduction of acres burned. It has not (Keeley and Fotheringham 2003). Although Pyne makes it clear multiple times that fire management techniques transfer poorly from one system to another, the reader will probably come away thinking dense, old-growth chaparral is "unhealthy" and needs to burn in the same way some overstocked Ponderosa pine forests do. This misconception unfortunately dominates public discourse and many fire management plans despite the lack of corroborating scientific evidence. The few remaining old-growth chaparral stands in California are in fact beautiful, dynamic communities that have been protected rather than created by successful fire suppression. This is important for agencies to understand in order to prevent these valuable natural resources from falling victim to overzealous vegetation treatments. Large tracts of chaparral have already been type-converted to alien grassland by increased fire frequency due to "range management" practices, accidental ignition, and arson. Introducing more fire into the system will only accelerate the process. The only place where prescribed fire and other vegetation management techniques make sense in California chaparral is in a strategic manner directly along the wildland/urban interface where homes exist next to wildlands.

In discussing our past relationship to fire, Pyne gives a bit too much credit to humans as agents of evolutionary change. While it is safe to assume early humans knew how to use fire to manipulate their environment, the extent and frequency is unknown. Humans have changed fire regimes wherever they have gone to be sure. However, it is impossible to separate natural from anthropogenic fires in prehistoric times. The role of humans in shaping the development of fire adapted species or ecosystems was likely minimal, especially in Australia and the Americas where *Homo sapiens* are recent arrivals.

The United States Forest Service, and the firefighters who work for it, are usually the ones singled out for causing the wildfire problems we see today. After the Great Fires of 1910, where three million acres burned in Idaho and Montana and 84 people died, the federal government embarked upon a major effort to suppress all fire as soon as possible in order to prevent such a disaster from occurring again. Conventional wisdom claims this effort was shortsighted and has led to excessive fuel loads and the growth of so-called dog hair forests. If we had only listened, the thinking continues, to the earliest fire ecologists, such as Herbert Stoddard and Harold Biswell, the extreme fire risks we currently see would not exist. Pyne takes these assumptions head on and deals with them in a balanced manner, pointing out that fire suppression is

only one of many factors contributing to the current condition of our nation's wildlands. He mentions logging, grazing, road building, land use policy, and the invasion of non-native species ("exotic pyrophytes like cheatgrass that rapidly remake landscapes in ways that promote undesired fire regimes") as having important impacts as well. "It is the sum of all we have done and not done over the past century," Pyne also cautions there is not a one-to-one correspondence between aggressive suppression and uncontrollable fuels because too many variables are involved from "wind, drought, and browsers."

Although fuel is obviously important, the arrangement of that fuel and the environmental conditions under which it burns will determine whether or not the flames become unmanageable. For example, underappreciated by the general public, but well known to firefighters, are the dangers of grass fires. The speed and intensity in which flames can move through weedy fields has cost the lives of many. Last year, California Department of Forestry firefighter Eva Schicke was killed during a 30 second burn over when a sudden wind change pushed flames into the grassy area she was trying to cross in order to reach the assigned safety zone. "The reason ignitions of any sort spread. . . is that the environment can propagate them, and this is mostly a consequence of short-term weather. Regional-scale bouts of drying and wind associated with the arrival and breakdown of high-pressure systems, events ranging from five to fourteen days, underwrite most of North America's extensive burns and explosive runs." It is important here to make the distinction between climate and local weather. Recent climate changes have had major impacts on increasing both the size and frequency of fires by reducing fuel moisture over much of the Western United States. Local weather influenced by wildfire behavior is one of the primary variables responsible for fire spread and firefighter fatalities.

In hindsight, it is easy to say that the government's response to the Great Fires of 1910 failed to properly consider all the consequences of fire suppression. However, there were and remain good reasons to fight wildfires quickly and aggressively; they kill people and destroy property. It is therefore inherently unfair to criticize fire fighting agencies for not letting fires burn "naturally" through forests while at the same time expecting them to do all they can to protect lives and communities through fire suppression. This is especially true when considering how poor land planning has resulted in the creation of a virtually unmanageable wildland/urban interface. This forces fire fighting agencies to defend often indefensible structures, thereby limiting their ability to actually control fire spread.

One of the issues that play a significant role in how wild and prescribed fires are managed is liability. "If a fire misbehaved, the government could

be sued," Pyne writes. The Australian fire model is discussed whereby citizens take an active role in protecting their communities, maintaining defensible space, and understanding fire behavior, but Pyne correctly points out that reforming American liability law (and attitudes about liability) would be necessary to successfully emulate such an approach. Perhaps more importantly, Australian governments more closely link fire managers in the land planning process.

Pyne also discusses various approaches to change the existing structure of both the US Forest Service and local fire fighting agencies to make for a more effective system of wildfire management. His organizational recommendations are a bit fuzzy, but he does make a good case for maintaining the bond between fire and land management. This is important because solving the wildfire problem can not be reduced to "thinning" of fuels. "In fact," Pyne writes, "the issue isn't trees, or grass, or elk, or Hereford cattle, or red-cockaded woodpeckers. It's about all of them. It's about making all the parts of the fire management mesh. It's about synchronizing fire practices with the land."

But even if all the issues could be resolved, Pyne makes it clear that big fires are ultimately unpreventable. They will happen because we will never be able to control all the variables. Acknowledgment of such a fact needs to be incorporated into public policy and the public needs to accept and understand the limits of fire fighting agencies. "Even the best systems will lose 2 to 3 percent of starts under extreme conditions, and these fires may sweep widely."

With his signature writing style, Pyne makes a plea for change in how we deal with wildfire by highlighting the fascinating nature of the subject and discussing the traditional schism that separates the fire community from the academic—ologists. "Partly this reflects a failure of intellectuals to see anything significant in the flames," he writes. "But mostly the chasm betrays a failure of the fire community to appreciate how the flames that it finds so compelling in the field . . . illuminate fascinating questions . . ." Because in studying fire, he continues, ". . . the mind can experience a rush as stirring as anything wrought by a torching fir."

—RICHARD W. HALSEY. The California Chaparral Field Institute, P.O. Box 545, Escondido, CA 92033.

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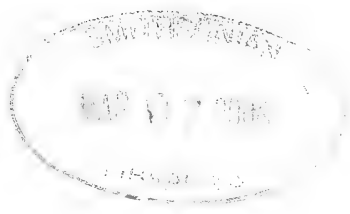
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Editor—DR. JOHN HUNTER
c/o UC Davis Herbarium/Center for Plant Diversity
Plant Biology
One Shields Avenue
University of California Davis
Davis, CA 95616
johnhunterca@sbcglobal.net

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VASCULAR FLORA OF GOLDEN AND SILVER FALLS STATE NATURAL AREA IN THE OREGON COAST RANGE, COOS COUNTY, OREGON

RALPH L. THOMPSON¹ AND JOHN R. SKEESE III

Herbarium, Biology Department, Berea College, Berea, KY 40404-2121

ABSTRACT

A descriptive plant survey was conducted of Golden and Silver Falls State Natural Area in the Coast Range northeast of Coos Bay in Coos County, Oregon, during 1988, 1990, and 1997. The 63.6 ha natural area was established in 1936 to preserve an old-growth stand of *Pseudotsuga menziesii* surrounding the area of two scenic waterfalls. Vascular flora consisted of 241 specific and infraspecific taxa in 162 genera from 61 families, of which 70 taxa (29 %) were exotics. The five plant habitats were steep coniferous mountain slopes (*Pseudotsuga menziesii*-*Tsuga heterophylla*/*Acer circinatum*/*Polystichum munitum* association) and (*Pseudotsuga menziesii*-*Tsuga heterophylla*/*Gaultheria shallon*/*Polystichum munitum* association), sandstone cliff escarpments, lowland valley hardwoods (*Acer macrophyllum*-*Umbellularia californica*/*Polystichum munitum* association), ruderal, and riparian floodplain (*Alnus rubra*/*Rubus spectabilis*/*Oxalis oregana* association).

Key Words: Flora, floristics, Golden and Silver Falls, natural area, Oregon, plant survey.

Golden and Silver Falls State Natural Area is a 63.6 ha topographically rugged and forested tract located about 38.7 km northeast of Coos Bay in Coos County within the Oregon Coast Range of southwestern Oregon (Fig. 1). The natural area, formerly Golden and Silver Falls State Park, is under the management of Sunset Bay State Park District of the Oregon Parks and Recreation Department.

Golden and Silver Falls State Park was originally established in 1936 to preserve an old-growth stand of *Pseudotsuga menziesii* on extremely steep sandstone terrain surrounding two scenic waterfalls within its boundaries, Golden Falls on Glenn Creek and Silver Falls on Silver Creek (Armstrong 1965). Golden Falls plummets 49 m over a series of sandstone rock walls and Silver Falls flows 37 m over an unusual dome-shaped sandstone projection (Plumb 1983).

The initial Golden Falls area, a tract of 45.3 ha, was acquired from the Waterford Lumber Company in June 1936. The Silver Falls area of 7.0 ha and 11.3 ha tracts were donated to the state by the Weyerhaeuser Timber Company in September 1938, and May 1955, respectively (Armstrong 1965).

Golden and Silver Falls State Natural Area was studied because the vascular plants were not documented, and there have been very few published botanical studies from the Oregon Coast Range (Chambers 1973; Greene 1982; Thompson 2001). Survey data provides baseline information on the presence, location, and abundance of the plant taxa as a contribution to the ongoing Oregon Flora Project at Oregon State University (Oregon Flora Project 2005) and for the use of park personnel and scientists. Major objectives were to document the

vascular flora with representative voucher specimens, provide an annotated list of species, and describe the habitats and their plant associations.

The study site description. Golden and Silver Falls State Natural Area, is located within the Oregon Coast Range Physiographic Province (Franklin and Dryness 1988) of the Mid-Coastal Sedimentary Ecoregion (Thiele et al. 1996). It is situated in T24S, R10W, sect. 18 S½ of the Golden Falls Quadrangle at approximately 42°29'05"N, and 123°55'52"W. Elevations range from 95 to 293 m.

Forested terrain within the perimeter of the natural area is composed of steep ravine slopes. A trail leads to Silver Falls and two trails, an upper and a lower one, lead to Golden Falls. A small picnic and parking area is located at the three trailheads. In the natural area, Silver Creek joins Glenn Creek which enters the East Fork of the Millicoma River 5 km downstream and eventually joins the Coos River leading to Coos Bay of the Pacific Ocean.

Sedimentary bedrock within Golden and Silver Falls State Park is classified as the Tyee Formation of Middle Eocene Age and is composed of thick rhythmically bedded, feldspathic and micaceous hard sandstone grading upward into thin-bedded sandstone and siltstone (Baldwin and Beaulieu 1973; Baldwin 1976). The sandstone formerly mapped as Tyee along Golden and Silver Falls has now been assigned to the White Tail Ridge Member of the Flournoy Formation (Baldwin 1981).

In the natural area, Preacher-Bohannon Mountain soils are found on moderately steep to very steep slopes (60–90 percent upper side slopes), ravines and ridgetops. These soils are deep to moderately deep, very gravelly sandy loams to gravelly and loamy soils formed in colluvium and residuum from the Eocene sandstones and siltstones. The Milbury-Bohannon-Umpcoos Association occupies

¹ Author for correspondence, email: ralph_thompson@berea.edu

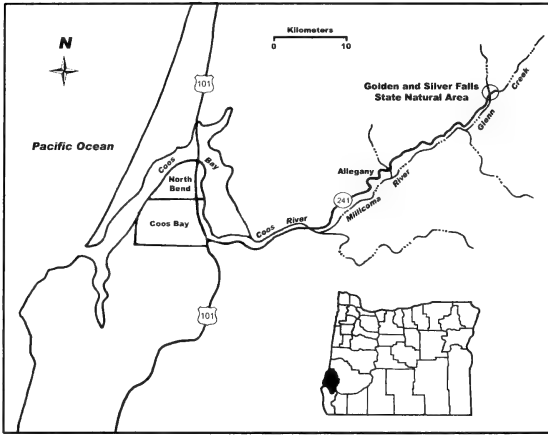


FIG. 1. Location of Golden and Silver Falls State Natural Area, in the Oregon Coast Range, northeast of Coos Bay, Coos County, Oregon.

50–80 percent lower side slopes adjacent to Silver Creek and Glenn Creek below the waterfalls and within the lower natural area boundary. Surface soils are blackish-brown gravelly, sandy loams 8–38 cm deep and typically covered with a mat of undecomposed litter 2.5–10 cm thick. Subsoils are grayish-brown, very cobbly loams from 33–86 cm deep. Hard consolidated to fractured, weathered sandstone and siltstone bedrock lies beneath the subsoils (Haagen 1989).

Köppen (2004) climate classification for the Oregon coast is Cool Marine West Coast. Climate in the Oregon Coast Range is characterized by mild winters with rain and fog precipitation because of moist mid-latitude cyclones. Summers are humid, dry, and short in duration. Precipitation is seasonal with a peak in November–January and a minimum in July–August. Climatic data are from North Bend FAA Airport, the closest weather station, 42 km south of Golden and Silver Falls (Oregon Climate Service 2002). Mean annual temperature is 11.5°C with a mean January temperature of 7.8°C and a mean July temperature of 15.7°C. Mean annual precipitation is 1636 mm, with mean a June through August rainfall of 79 mm. The mean growing season is 288 days, with the median first freeze on November 1, and the median last freeze on April 19.

Forest vegetation of the Oregon Coast Range within the Golden and Silver Falls State Natural Area is classified within the *Thuja-Tsuga-Pseudotsuga* Forest of Küchler (1964) and the *Tsuga heterophylla* Zone of Franklin and Dyrness (1988). In the natural area, *Pseudotsuga menziesii* is the dominant overstory tree with many fewer *Tsuga heterophylla* and some *Thuja plicata* throughout the steep mountain slopes. Canopy hardwoods at lower elevations along Silver Creek and Glenn Creek include *Acer macrophyllum*, *Alnus rubra*, and *Umbellularia californica*.

METHODS

Vascular plants were collected from April–October in 1988, 1990, and 1997. Representative voucher specimens were deposited in the Oregon State University Herbarium (OSC), Corvallis. References for plant identifications were Hickman (1993) and Hitchcock and Cronquist (1973). Classification and nomenclature follow Hickman (1993).

Data was collected on origin of taxa (exotic or native), plant habitats, associated species, and relative abundance. Plant associations were determined from habitat, physiognomy, and dominant species of the canopy, subcanopy, shrub, and herb layers. Plant associations within habitats were named according to their major dominant overstory and understory indicator species. These plant associations were adapted from the classification of native vegetation of Oregon by Kagan et al. (2004).

Relative abundance was determined through field observations of number of individuals or colonies for each taxon. A single relative abundance value was assigned to each taxon. Relative abundance categories adapted from Thompson (2001) are: *Rare* (R)—1 to 5 individuals or colonies in the natural area; *Infrequent* (I)—6 to 30 individuals or colonies; *Occasional* (O)—31 to 100 individuals or colonies; *Frequent* (F)—101 to 1000 individuals or colonies; and *Abundant* (A)—more than 1000 individuals or colonies.

RESULTS AND DISCUSSION

Taxonomic Summary

The vascular flora consists of 241 specific and infraspecific taxa in 162 genera from 61 families. Seventy (29 %) are exotics (Table 1). Species were classified into two Equisetophyta, one Lycopodiophyta, nine Polypodiophyta, three Pinophyta, and 226 Magnoliophyta taxa (Table 1; Appendix I). By growth form, 59 were annuals/biennials and 182 were perennials of which 30 were woody taxa. Species richness was greatest in Poaceae (30), Asteraceae (25), Fabaceae (15), Saxifragaceae (12), Juncaceae (11), and Liliaceae (9). Largest genera were *Juncus* (9), *Trifolium* (7), *Carex* (5), *Rubus* (5), and *Saxifraga* (4) (Appendix I).

Habitats and Plant Associations

Five habitats were recognized from physical features and vegetation. Many species were not confined to any single plant habitat or association and considerable intergrading occurred in ecotonal areas; however, changes in species dominance, distribution, growth form, and habitat gave each association a recognizable physiognomy.

1. *Steep Coniferous Mountain Slopes*. The most extensive habitat within the natural area consisted of steep sandstone mountain slopes that encompass several topographic slope aspects. The vegetation

TABLE 1. CLASSIFICATION OF VASCULAR PLANTS AT GOLDEN AND SILVER FALLS STATE NATURAL AREA, OREGON.

| Division | Families | Genera | Species | Native | Exotic | Species Composition Percent |
|----------------|----------|--------|---------|--------|--------|-----------------------------------|
| Equisetophyta | 1 | 1 | 2 | 2 | 0 | 0.83 |
| Lycopodiophyta | 1 | 1 | 1 | 1 | 0 | 0.41 |
| Polypodiophyta | 6 | 9 | 9 | 9 | 0 | 3.75 |
| Pinophyta | 2 | 3 | 3 | 3 | 0 | 1.24 |
| Magnoliophyta | 51 | 147 | 226 | 156 | 70 | 93.77 |
| Magnoliopsida | 45 | 111 | 165 | 113 | 52 | 68.46 |
| Liliopsida | 6 | 37 | 61 | 43 | 18 | 25.31 |
| Totals | 61 | 161 | 241 | 171 | 70 | 100.00 |

of this habitat was comprised principally of the *Pseudotsuga menziesii*-*Tsuga heterophylla*/*Acer circinatum*/*Polystichum munitum* association on northeastern, northwestern, and western slopes. The dominant *Pseudotsuga menziesii* was present in all size-classes. Important trees scattered throughout the steep slopes in smaller size-classes were *Tsuga heterophylla* and *Thuja plicata*. Small trees and shrubs included *Acer circinatum*, *Corylus cornuta*, *Holodiscus discolor*, *Rhamnus purshiana*, *Rhododendron macrophyllum*, *Rubus parviflorus*, and *R. spectabilis*.

Polystichum munitum was the predominant herbaceous species. Other ferns were *Adiantum aleuticum*, *Athyrium felix-femina*, *Blechnum spicant*, *Cystopteris fragilis*, and *Pteridium aquilinum*. Characteristic herbs included *Achlys triphylla*, *Actaea rubra*, *Asarum caudatum*, *Bromus vulgaris*, *Carex hendersonii*, *Dicentra formosa*, *Disporum smithii*, *Elymus glaucus*, *Maianthemum dilatatum*, *Smilacina racemosa*, *Trientalis latifolia*, *Trillium ovatum*, and *Vancouveria hexandra*.

On southwestern and southeastern-trending middle and lower slopes between the two waterfalls and the upper Golden Falls trail was the *Pseudotsuga menziesii*-*Tsuga heterophylla*/*Gaultheria shallon*/*Polystichum munitum* association. The understory was dominated by *Gaultheria shallon* and *Rhododendron macrophyllum* and included *Acer circinatum*, *Berberis nervosa*, *Corylus cornuta*, *Rubus parviflorus*, *R. spectabilis*, *Toxicodendron diversilobum*, *Vaccinium ovatum*, and *V. parvifolium*. At the top of the Golden Falls trail, *Arbutus menziesii* and *Arctostaphylos columbiana*, were also present. A similar, but greater herbaceous species richness existed in this association than in the *Pseudotsuga menziesii*-*Tsuga heterophylla*/*Acer circinatum*/*Polystichum munitum* association. These two associations abutt the *Acer macrophyllum*-*Umbellularia californica*/*Rubus parviflorus*/*Polystichum munitum* association and the *Alnus rubra*/*Rubus spectabilis*/*Oxalis oregana* association.

2. Sandstone Cliff Escarpments. The most exposed habitat was the south to northeast-trending vertical sandstone cliffs or rocky outcrops at the

crests of steep mountain slopes of Golden Falls and Silver Falls. In moisture availability, these cliffs ranged from exposed xeric to mesic-shaded areas. Colluvial soil material had collected on ledges, crevices, cracks, and in seasonally wet depressions. Woody species established on the steep cliffs included *Arctostaphylos columbiana*, *Garrya elliptica*, *Holodiscus discolor*, *Lonicera hispidula*, *Ribes sanguineum*, and *Toxicodendron diversilobum*.

Several characteristic herbaceous plants of these cliffs included *Aquilegia formosa*, *Asplenium trichomanes*, *Boykinia occidentalis*, *Clarkia amoena*, *Eriogonum nudum*, *Fritillaria lanceolata*, *Heuchera micrantha*, *Iris tenax*, *Lilium columbianum*, *Lomatium utriculatum*, *Mitella ovalis*, *Nemophila menziesii*, *Phacelia nemoralis*, *Saxifraga* spp., *Sedum spathulifolium*, and *Selaginella oregana*.

3. Lowland Valley Hardwoods. An evergreen hardwood and deciduous hardwood forest habitat was along the Silver Creek trail, lower Golden Falls trail, around part of the ruderal habitat, and adjacent to the riparian floodplain habitat at the junction of Silver and Glenn Creeks. This lower elevation habitat was representative of an *Acer macrophyllum*-*Umbellularia californica*/*Rubus parviflorus*/*Polystichum munitum* association. The overstory was predominantly *Umbellularia californica* in sapling, pole, and mature size-classes with pole-sized and mature *Acer macrophyllum* along the Silver Falls trail and the Golden Falls lower trail. The dominant shrub was *Rubus parviflorus*. Other small trees and shrubs were *Acer circinatum*, *Corylus cornuta*, *Rubus discolor*, *R. laciniatus*, *R. spectabilis*, *Sambucus racemosa*, and *Vaccinium parviflorum*.

The predominant herbaceous species was *Polystichum munitum*. Other ferns were *Athyrium filix-femina*, *Blechnum spicant*, *Cystopteris fragilis*, and *Polypodium glycyrrhiza* on tree trunks and branches of *Umbellularia californica* and *Acer macrophyllum*. The herbaceous layer had a high species richness. Characteristic herbs included *Carex deweyana*, *Circaea alpina*, *Claytonia sibirica*, *Galium triflorum*, *Hydrophyllum tenuipes*, *Luzula comosa*, *Montia parvifolia*, *Osorhiza chilensis*, *Oxalis oregana*, *O. suksdorfii*, *Stachys ajugoides*, *Tellima*

grandiflora, *Trientalis latifolia*, *Urtica dioica*, and *Viola glabella*.

4. *Ruderal Areas*. The ruderal habitat was comprised of anthropogenically-influenced areas without any permanent forest structure. This habitat included the open mowed yard and picnic area, the three waterfall trailheads, Golden Falls trail at the top of the falls, the Coos County roadside, and other disturbed ground adjacent to the *Acer macrophyllum-Umbellularia californica/Rubus parviflorus/Polystichum munitum* association.

The flora included a weedy assemblage of exotic and native species with many species from the Asteraceae, Fabaceae, and Poaceae. Characteristic herbaceous species included *Anaphalis margaritacea*, *Anthoxanthum odoratum*, *Bellis perennis*, *Cardamine oligosperma*, *Crepis capillaris*, *Cynosurus echinatus*, *Daucus carota*, *Digitalis purpurea*, *Hypochaeris radiata*, *Juncus tenuis*, *Lapsana communis*, *Leucanthemum vulgare*, *Lolium perenne*, *Lotus purshianus*, *Medicago lupulina*, *Plantago lanceolata*, *P. major*, *Poa annua*, *P. trivialis*, *Ranunculus repens*, *Rumex obtusifolius*, *Senecio* spp., *Stellaria media*, *Taraxacum officinale*, and *Trifolium* spp.

5. *Riparian Floodplain*. The Glenn Creek and Silver Creek riparian floodplain includes eroded creekbanks and alluvial cobble, gravel, and sandbar areas. This riparian habitat was occupied predominantly by the *Alnus rubra/Rubus spectabilis/Oxalis oregana* association. It adjoins the *Acer macrophyllum-Umbellularia californica/Rubus parviflorus/Polystichum munitum* association and the *Pseudotsuga menziesii-Tsuga heterophylla/Acer circinatum/Polystichum munitum* association. *Alnus rubra* was the major overstory hardwood at lower elevations along Glenn Creek and Silver Creek. Interspersed *Salix scouleriana*, *S. sitchensis*, *Acer macrophyllum*, and *Umbellularia californica* were also present. Characteristic shrubs and vines included *Rubus discolor*, *R. laciniatus*, *R. parviflorus*, *R. spectabilis*, *R. ursinus*, and *Sambucus racemosa*.

Several species of riparian areas were members of the Cyperaceae, Juncaceae, and Poaceae. *Phalaris arundinacea* was an important exotic species. Characteristic herbaceous species included *Agrostis* spp., *Carex interrupta*, *C. obnupta*, *Claytonia sibirica*, *Digitalis purpurea*, *Eleocharis obtusa*, *Epiobium ciliatum*, *Equisetum arvense*, *E. telmateia*, *Glyceria elata*, *Juncus* spp., *Mimulus moschatus*, *Oenanthse sarmentosa*, *Oxalis oregana*, *Polygonum hydropiper*, *Ranunculus repens*, *Scirpus microcarpus*, and *Tolmiea menziesii*.

CONCLUSIONS

Golden and Silver Falls State Natural Area is a remarkable state natural area that has been permanently set aside for preservation, research, and recreational purposes. The predominant vegetation of the natural area is an old-growth *Pseudotsuga men-*

ziesii forest. Two hundred forty-one vascular plant taxa are present in five diverse habitats within the natural area boundaries. This species richness is the result of the interrelation of various environmental and ecological factors that includes topographic-moisture gradients, soils, parent materials, lithology, physiognomy, slope aspect, insolation, and anthropogenic disturbances. This study is a contribution to the Oregon Vascular Plant Checklist and Oregon Plant Atlas of the Oregon Flora Project, Oregon State University.

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APPENDIX 1

ANNOTATED LIST OF VASCULAR PLANTS

This annotated list is arranged alphabetically by family and species. An asterisk (*) precedes an introduced or naturalized exotic species. The scientific name is followed by the plant habitat(s). Plant habitats are assigned a numbered code: 1 = Steep Coniferous Mountain Slopes; 2 = Sandstone Cliff Escarpments; 3 = Lowland Valley Hardwoods; 4 = Ruderal; and, 5 = Riparian Floodplain. A relative abundance value follows the plant habitat designation. An italicized plant collection number is given after the relative abundance value.

EQUISETOPHYTA

Equisetaceae

Equisetum arvense L. 5; I. 90-631.

Equisetum telmateia Ehrh. ssp. *braunii* (Milde) R. L. Hauke 3, 4, 5; F. 90-102

LYCOPODIOPHYTA

Selaginellaceae

Selaginella oregana D. C. Eaton 1; F. 97-93

POLYPODIOPHYTA

Aspleniaceae

Asplenium trichomanes L. ssp. *trichomanes* 2; I. 90-545

Blechnaceae

Blechnum spicant (L.) Smith 1, 3, 5; F. 97-78

Dennstaedtiaceae

Pteridium aquilinum (L.) Kuhn. var. *pubescens* Underw. 1, 3, 4; F. 88-1384

Dryopteridaceae

Athyrium filix-femina (L.) Roth var. *cyclosorum* Rupr. 1, 3; F. 88-1687

Cystopteris fragilis (L.) Bernh. 1, 3; I. 88-1411

Polystichum munitum (Kaulf.) Presl. 1, 3, 4; A. 97-68

Polypodiaceae

Polypodium glycyrrhiza D. C. Eaton 1, 3, 5; O. 97-72

Pteridaceae

Adiantum aleuticum (Rupr.) C.A. Paris 1, 3; O. 90-143

Pentagramma triangularis (Kaulf.) Yatskievych, Windham, & Wollenweber ssp. *triangularis* 1; I. 97-92

PINOPHYTA

Cupressaceae

Thuja plicata D. Don. 1, 3; O. 97-94

Pinaceae

Pseudotsuga menziesii (Mirbel) Franco var. *menziesii* 1, 2, 3; A. 97-104

Tsuga heterophylla (Raf.) Sarg. 1, 2; A. 97-99

MAGNOLIOPHYTA-MAGNOLIOPHYTA

Aceraceae

Acer circinatum Pursh 1, 3, 5; A. 88-1415

Acer macrophyllum Pursh 1, 3, 5; F. 90-146

Anacardiaceae

Toxicodendron diversilobum (Torr. & A. Gray) E. Greene 1, 2; F. 90-653

Apiaceae

**Daucus carota* L. 4; I. 88-1831

Lomatium utriculatum (Torr. & A. Gray) Coult. & Rose 2; O. 97-83

Oenanthe sarmentosa J. S. Presl. 3, 5; O. 88-1838

Osmorhiza chilensis Hook & Arn. 3; O. 90-528

**Torilis arvensis* (Hudson.) Link 4; O. 88-1420

Aristolochiaceae

Asarum caudatum Lindl. 1, 3; O. 88-1157

Asteraceae

Achillea millefolium L. 4; O. 88-1464

Adenocaulon bicolor Hook. 3, 4; F. 88-1656

Anaphalis margaritacea (L.) Benth. & Hook. 3, 4; O. 88-1690

Arnica chamissonis Less. ssp. *foliosa* (Nutt.) Maguire 3; I. 88-1693

**Bellis perennis* L. 4; O. 97-74

**Cichorium intybus* L. 4; R. 88-1642

Cirsium edule Nutt. 4; I. 88-1603

Cirsium remotifolium (Hook.) DC. 4; I. 88-1463

**Crepis capillaris* (L.) Wallr. 4; O. 90-625

**Erechtites minima* (Poir.) DC. 4; I. 90-636

Erigeron annuus (L.) Pers. 4; I. 88-1658

Eriophyllum lanatum (Pursh) J. Forbes var. *lanatum* 2; I. 88-1766

**Gnaphalium japonicum* Thunb. 4; R. 88-1808

Hieracium albiflorum Hook. 4; O. 88-1801

**Hypochaeris radicata* L. 4; F. 90-628

**Lapsana communis* L. 4; O. 90-576

**Leucanthemum vulgare* Lam. 4; F. 88-1160

Madia gracilis (J. E. Smith) Keck 2; I. 88-1768

Petasites frigidus (L.) Fries var. *palmaris* (Ait.) Cronq. 4; I. 97-71

**Senecio jacobaea* L. 4; I. 90-637

**Senecio sylvaticus* L. 4; O. 88-1847

**Senecio vulgaris* L. 4; I. 90-139

**Sonchus asper* (L.) Hill ssp. *asper* 4; O. 88-1465

**Sonchus oleraceus* L. 4; I. 88-1824

**Taraxacum officinale* Wigg. 4; O. 97-80

Berberidaceae

Achlys triphylla (Smith) DC. ssp. *triphylla* 1; O. 90-602

Berberis nervosa Pursh 2; O. 90-558

Vancouveria hexandra (Hook.) Morren & Decne. 1, 3; O. 90-507

Betulaceae

Alnus rubra Bong. 3, 5; A. 97-70

Corylus cornuta Marsh. var. *californica* (A. DC.) W. Sharp 1, 3, 5; F. 88-1413

Brassicaceae

Cardamine californica (Torr. & A. Gray) var. *sinuata* (E. Greene) O. Schulz. 1, 34; O.

97-62

**Cardamine hirsuta* L. 4; I. 90-114

Cardamine occidentalis (Robinson) Howell 3; 4; F. 97-62

Cardamine oligosperma Torr. & A. Gray 1, 3; O. 97-64

**Raphanus raphanistrum* L. 4; R. 88-1851

**Sisymbrium officinale* (L.) Scop. 4; R. 90-633

Campanulaceae

Campanula prenanthoides Durand 2; R. 90-577

Campanula scouleri Engelm. 2; I. 88-1762

Caprifoliaceae

Lonicera hispidula (Lindl.) Dougl. var. *hispidula* 1, 4; I. 90-581

Sambucus racemosa L. var. *arborescens* (Torr. & A. Gray) McMin. 3, 5; O. 88-1611

Caryophyllaceae

Cerastium arvense L. 4; R. 88-1616

**Cerastium fontanum* Baumg. ssp. *vulgare* (Hartman) Greuter & Burdet 4; O. 88-1623

**Cerastium glomeratum* Thuill. 4; I. 90-130

Sagina procumbens L. 4, 5; I. 88-1616

**Spergula arvensis* L. var. *arvensis* 4; R. 90-612

Stellaria longipes Goldie var. *longipes* 5; R. 88-1616

**Stellaria media* (L.) Villars 4, 5; F. 90-622

Convolvulaceae

**Calystegia sepium* (L.) R. Br. 5; I. 88-1655

Crassulaceae

Sedum spathulifolium Hook. 2; O. 90-586

Cucurbitaceae

Marah oreganus (Torr. & A. Gray) Howell 3, 6; O. 90-502

Ericaceae

Arbutus menziesii Pursh 1; I. 90-610

Arctostaphylos columbiana Piper 1; 2; O. 88-1691

Gaultheria shallon Pursh 1, 3; A. 88-1839

Monotropa uniflora L. 1; R. 97-102

Rhododendron macrophyllum D. Don 1; F. 88-1163

Vaccinium ovatum Pursh 1; F. 88-1188

Vaccinium parvifolium Smith 1, 2; F. 90-511

Fabaceae

Lathyrus sulphureus A. Gray 4; R. 88-1840

Lotus micranthus Benth. 4; I. 88-1800

Lotus purshianus (Benth.) Clem. & Clem. var. *purshianus* 4; O. 88-1682

**Lotus uliginosus* Schk. 4; I. 90-635

Lupinus rivularis Lindl. 5; R. 90-578

**Medicago lupulina* L. 4, 5; O. 88-1604

**Trifolium dubium* Sibth. 4, 5; O. 90-503

Trifolium microcephalum Pursh 5; I. 88-1821

Trifolium oliganthum Steud. 2; 4; I. 88-1775

**Trifolium pratense* L. 4; I. 88-1143

**Trifolium repens* L. 4; O. 88-1620

Trifolium variegatum Nutt. 3, 4; I. 90-551

Trifolium willdenovii Sprengel. 4; I. 88-1377

**Vicia tetrasperma* (L.) Schreb. 4; R. 88-1754

**Vicia sativa* L. ssp. *nigra* (L.) Erhart. 4; R. 88-1379

Garryaceae

Garrya elliptica Lindl. 2; I. 97-95

Gentianaceae

**Centaurium erythraea* Raf. 4; I. 88-1387

Geraniaceae

**Geranium dissectum* L. 4; O. 88-1640

**Geranium molle* L. 4; O. 90-521

Grossulariaceae

Ribes lacustre (Pers.) Poir. 3; R. 88-1647

Ribes sanguineum Pursh 1, 2; I. 97-82

Hydrophyllaceae

Hydrophyllum tenuipes A. A. Heller 1, 3; F. 90-543

Nemophila menziesii Hook. & Arn. var. *atomaria* (Fischer & Mey.) Chandler 2; O.

97-65

Nemophila parviflora Benth. 2; R. 88-1426

Phacelia nemoralis E. Greene ssp. *oregonensis* Heckard 2, 4; F. 90-504

Romanzoffia californica E. Greene 2; O. 90-137

Hypericaceae

**Hypericum perforatum* L. 4; I. 88-1441

Lamiaceae

**Lamium purpureum* L. 4; I. 97-67

**Prunella vulgaris* L. var. *lanceolata* (Barton) Fern. 3; 4; O. 90-512

Stachys ajugoides Benth. var. *rigida* Jepson & Hoover 3, 5; F. 90-580

Lauraceae

Umbellularia californica (Hook. & Arn.) Nutt. 3, 4, 5; F. 90-124

Linaceae

**Linum bienne* P. Mill. 4; R. 88-1443

Malvaceae

Sidalcea malvaeflora (DC.) A. Gray ssp. *virgata* (Howell) C. Hitchc. 2; R.

90-583

Onagraceae

Circaea alpina L. ssp. *pacifica* (Asch. & Magnus) Raven 1, 3; O. 90-538

Clarkia amoena (Lehm.) Nelson & J. F. Macbr. ssp. *huntiana* (Jepson)

H. Lewis & M. Lewis 2; I. 88-1694

Epilobium brachycarpum C. Presl. 2; O. 88-1830

Epilobium ciliatum Raf. ssp. *watsonii* (Barbey) P. Hoch & Raven 3, 5; F. 90-644

Epilobium minutum Lehm. 4, 5; I. 88-1439

Orobanchaceae

Orobanche uniflora L. var. *purpurea* (A.A. Heller) D.C. Achey 1; R. 90-142

Oxalidaceae

Oxalis oregana Nutt. 1, 3, 4, 5; A. 97-69

Oxalis suksdorfii Trel. 1, 3; O. 90-613

Oxalis trilliifolia Hook. 1, 3; O. 90-594

Papaveraceae

Dicentra formosa (Haw.) Walp. 1, 2, 3; F. 90-532

Plantaginaceae

**Plantago lanceolata* L. 4; O. 97-88

**Plantago major* L. 4; O. 90-621

Polemoniaceae

Collomia heterophylla Hook. 2; O. 88-1764

Gilia capitata Sims ssp. *capitata* 2; I. 90-584

Polygonaceae

Eriogonum nudum Benth. 2; O. 88-1823

**Polygonum hydropiper* L. 5; F. 90-627

**Polygonum persicaria* L. 4, 5; O. 90-630

**Rumex acetosella* L. 2, 4; O. 88-1901

**Rumex obtusifolius* L. 4, 5; O. 88-1848

Portulacaceae

Claytonia sibirica L. 3; 4, 5; F. 97-61

Montia parvifolia (DC.) E. Greene 1, 3, 4, 5; A. 97-91

Primulaceae

**Anagallis arvensis* L. 4; R. 88-535

Trientalis latifolia Hook. 1, 3; O. 90-544

Ranunculaceae

Actaea rubra (Ait.) Willd. 1, 3; I. 88-1811

- Anemone deltoidea* Hook. 1; R. 88-1417
Aquilegia formosa Fisch. 1, 2; O. 88-1194
Delphinium trolliifolium A. Gray 3; I. 88-1205
**Ranunculus repens* L. 3, 4, 5; F. 90-515
Ranunculus uncinatus D. Don var. *parviflorus* (Torr.) L. Benson 1, 3; O. 90-537
- Rhamnaceae
Rhamnus purshiana DC. 1, 2; F. 88-1388
- Rosaceae
Aruncus dioicus (Walt.) Fern. var. *pubescens* (Rydb.) Fern. 3, 5; O. 90-593
Holodiscus discolor (Pursh) Maxim. 1, 2, 3; F. 90-541
Rosa gymnocarpa Nutt. 1, 3; I. 90-556
**Rubus discolor* Weihe & Nees 4, 5; F. 88-1398
**Rubus laciniatus* Willd. 1, 4; O. 90-590
Rubus parviflorus Nutt. 1, 3, 4, 5; F. 90-540
Rubus spectabilis Pursh 1, 3, 4, 5; A. 97-103
Rubus ursinus Cham. & Schledl. 3, 4; F. 88-1407
- Rubiaceae
**Galium aparine* L. 3, 4; O. 88-1146
Galium triflorum Michx. 1, 3, 4; F. 90-639
- Salicaceae
Salix scouleriana Hook. 3, 5; O. 88-1389
Salix sitchensis Bong. 3, 5; F. 90-642
- Saxifragaceae
Boykinia occidentalis Torr. & A. Gray 2, 3; F. 90-643
Chrysosplenium glechomifolium Nutt. 2, I. 88-1132
Heuchera micrantha Lindl. 2; O. 90-509
Mitella caulescens Nutt. 2; I. 88-1162
Mitella ovalis E. Greene 2; F. 90-118
Saxifraga marshallii E. Greene 2; F. 97-90
Saxifraga mertensiana Bong. 2; R. 88-1451
Saxifraga nuttallii Small 2; O. 90-132
Saxifraga occidentalis Wats. 2; O. 90-140
Tellima grandiflora (Pursh) Lind. 3, 5; O. 90-523
Tiarella trifoliata L. var. *trifoliata* 2; R. 88-1760
Tolmiea menziesii (Pursh) Torr. & A. Gray 2, 3; F. 90-518
- Scrophulariaceae
**Digitalis purpurea* L. 1, 2, 4, 5; F. 90-588
Mimulus dentatus Benth. 3, 5; O. 90-522
Mimulus guttatus DC. 3, 4, 5; F. 97-66
Mimulus moschatus Lindl. 3, 5; F. 88-1849
**Parentucellia viscosa* (L.) Caruel. 4; I. 88-1649
Synthyris reniformis (Dougl.) Benth. 1, 3; O. 97-84
Veronica americana (Raf.) Schwein. 3, 5; I. 90-526
**Veronica serpyllifolia* L. ssp. *humifusa* (Dickson) Syme. 4, 5; I. 90-546
- Urticaceae
Urtica dioica L. ssp. *gracilis* (Ait.) Seland. 3, 5; F. 88-1196
- Valerianaceae
Plectritis congesta (Lindl.) A. DC. 2; R. 88-1131
- Violaceae
Viola glabella Nutt. 3, 5; F. 97-75
- MAGNOLIOPHYTA-LILIOPSIDA
- Cyperaceae
Carex deweyana Schwein 3; O. 90-595
Carex hendersonii L. Bailey 1, 2; O. 90-533
Carex interrupta Boeck. 5; O. 88-1212
Carex nudata W. Boott 5; I. 88-1381
Carex obnupta L. Bailey 5; I. 88-1179
Eleocharis obtusa (Willd.) Schult. var. *obtusa* 5; O. 88-1845
- Scirpus microcarpus* C. Presl. 5; F. 88-1666
- Iridaceae
Iris tenax Dougl. 1, 2; I. 90-510
- Juncaceae
Juncus articulatus L. 5; O. 88-1857
Juncus bolanderi Engelm. 5; O. 90-618
Juncus bufonius L. 5; O. 90-634
Juncus covillei Piper 3, 5; I. 88-1664
Juncus effusus L. var. *gracilis* Hook. 5; R. 90-629
Juncus effusus L. var. *pacificus* Fern. & Wieg. 5; O. 90-616
Juncus ensifolius Wikström. 5; O. 90-619
Juncus patens E. Meyer 5; O. 88-1657
Juncus tenuis Willd. 4, 5; F. 88-1667
Luzula comosa E. Meyer 1, 3; O. 90-585
Luzula parviflora (Ehrh.) Desv. 1, 3; O. 90-520
- Liliaceae
Brodiaea elegans Hoover. 2; R. 88-1767
Disporum smithii (Hook.) Piper 1, 3; O. 90-529
Fritillaria affinis (Schultes) Sealy. 2; I. 97-85
Lilium columbianum Baker 2; R. 88-1302
Maianthemum dilatatum (Alph. Wood) Nelson & Macbr. 1, 3; O. 90-513
Smilacina racemosa (L.) Link 1, 3; O. 88-1833
Streptopus amplexifolius (L.) DC. var. *americanus* Schult. 1, 3; I. 90-601
Trillium ovatum Pursh ssp. *ovatum* 1, 3; O. 97-86
Triteleia hyacinthina (Linds.) E. Greene 2; R. 88-1692
- Orchidaceae
Epipactis gigantea Hook. 7; I. 88-1442
Goodyera oblongifolia Raf. 1; I. 90-144
Piperia elegans (Lindl.) Rydb. ssp. *elegans* 2; R. 88-1757
- Poaceae
**Agrostis capillaris* L. 3, 5; F. 90-579
Agrostis exarata Trin. 3; O. 90-617
**Agrostis gigantea* Roth 3; I. 88-1169
**Aira caryophylla* L. 3, 4; O. 88-1130
**Anthoxanthum odoratum* L. 4; I. 88-1125
**Briza minor* L. 4; R. 88-1478
**Bromus diandrus* Roth 4; I. 88-1479
**Bromus hordeaceus* L. 4; O. 88-1494
Bromus vulgaris (Hook.) Shear. 1; F. 90-578
**Cynosurus cristatus* L. 4; O. 88-1475
**Cynosurus echinatus* L. 4; O. 90-624
**Dactylis glomerata* L. 4; O. 88-1686
Descampsia elongata (Hook.) Munro 3, 5; I. 88-1477
Elymus glaucus Buckl. 1, 3; O. 90-645
**Elytrigia repens* (L.) Nevski. 4; R. 88-1476
Festuca occidentalis Hook. 1, 3; O. 90-501
Festuca subulata Trin. 3; O. 90-530
Festuca subuliflora Schribn. 3; R. 88-1126
Glyceria elata (Lam.) A. Hitchc. 3, 5; F. 90-555
Hierochloa occidentalis Buckl. 1; O. 97-89
**Holcus lanatus* L. 3, 4; O. 90-638
**Lolium multiflorum* Lam. 4; O. 88-1837
**Lolium perenne* L. 4; I. 90-534
**Phalaris arundinacea* L. 3, 5; A. 88-1628
**Poa annua* L. 4; F. 97-81
Poa laxiflora Buckl. 3; R. 88-1166
**Poa trivialis* L. 4, 5; F. 90-524
Torreyochloa pallida (J. S. Presl) Church var. *pauciflora* (J. S. Presl) J. I. Davis 5; R. 88-1842
Tritisetum canescens Buckl. 3; R. 88-1496
**Vulpia myuros* (L.) C. Gmel. 4; O. 88-1171

SERPENTINE ENDEMISM IN THE CALIFORNIA FLORA: A DATABASE OF SERPENTINE AFFINITY

H. D. SAFFORD^{1,2}, J. H. VIERS³, AND S. P. HARRISON²

¹ USDA-Forest Service, Pacific Southwest Region, 1323 Club Drive,
Vallejo, CA 94592

hughsafford@fs.fed.us

² Department of Environmental Science and Policy, University of California,
Davis, CA 95616

³ Information Center for the Environment, DESP, University of California,
Davis, CA 95616

ABSTRACT

We present a summary of a database documenting levels of affinity to ultramafic (“serpentine”) substrates for taxa in the California flora, USA. We constructed our database through an extensive literature search, expert opinion, field observations, and intensive use of accession records at key herbaria. We developed a semi-quantitative methodology for determining levels of serpentine affinity (strictly endemic, broadly endemic, strong “indicator”, etc.) in the California flora. In this contribution, we provide a list of taxa having high affinity to ultramafic/serpentine substrates in California, and present information on rarity, geographic distribution, taxonomy, and lifeform. Of species endemic to California, 12.5% are restricted to ultramafic substrates. Most of these taxa come from a half-dozen plant families, and from only one or two genera within each family. The North Coast and Klamath Ranges support more serpentine endemics than the rest of the State combined. 15% of all plant taxa listed as threatened or endangered in California show some degree of association with ultramafic substrates. Information in our database should prove valuable to efforts in ecology, floristics, biosystematics, conservation, and land management.

Key Words: serpentine, ultramafic, California, endemism, diversity.

INTRODUCTION

Ultramafic rocks, often called “serpentine” by ecologists, botanists and pedologists, underlie more than 6000 km² of the land area of the State of California (Harrison et al. 2000). The edges of continental plates often include bands of these vestiges of oceanic mantle rock, accreted during the geologic process of subduction, and later uplifted and exposed during mountain building and subsequent erosion. Ultramafic rocks and the soils that develop on them are characterized by critically low levels of most principal plant nutrients (N, P, K, Ca), and exceptionally high levels of Mg and Fe and a suite of toxic trace elements including Cr, Ni, and Co. Outcrops of ultramafic rocks support high numbers of edaphic-endemic taxa throughout the world (Brooks 1987). The California serpentine flora is the richest in the temperate zone, and consists of hundreds of species and subspecies that are largely or entirely confined to ultramafic substrates.

Serpentine endemism is a key feature of the diversity of the California flora (Raven and Axelrod 1978; Kruckeberg 2002). Of about 1410 full species endemic to the State (Hickman 1993), Kruckeberg (1984) estimated that about 180 were endemic to serpentine. If these numbers are at least approximately correct, then about 13% of the plant species endemic to California are serpentine endemics. This is a remarkably high number when one considers that only 1.5% of the State is under-

lain by ultramafic rocks (6000 km²/406,280 km²). In addition, because they tend to have small geographic ranges and because many of them occur in the rapidly urbanizing San Francisco Bay Area, serpentine endemics are overrepresented among the state’s rare, sensitive, and listed plant taxa (Skinner and Pavlik 1994). The ecology of California’s serpentine plants has been extensively studied at the University of California’s Sedgwick Ranch Reserve (e.g., Seabloom et al. 2003; Gram et al. 2004) and McLaughlin Reserve (e.g., Harrison et al. 2003; Safford and Harrison 2004) and Stanford University’s Jasper Ridge Reserve (e.g., McNaughton 1968; Huenneke et al. 1990; Hobbs and Mooney 1991).

Botanists have relied for two decades on the monograph by Arthur Kruckeberg (1984) for most of their information on Californian serpentine-endemic plant taxa. Since then, publication of the Jepson Manual (Hickman 1993), and a proliferation of new botanical research and name changes have left this list in need of updating. Our initial aim was to modify Kruckeberg’s (1984) list, primarily using information from Hickman (1993), to use in our research on diversity patterns (Harrison et al. 2000, 2004). However, it soon became clear that we would have to expand and intensify our search for the best available information. Complicating this effort, plants show a continuum in degrees of serpentine restriction, and are sometimes more restrict-

ed in some parts of their geographic ranges than others, thus contributing to inconsistencies among reports from different sources. This led us to adopt a semi-quantitative procedure for scoring plant taxa on their reported degree of serpentine affinity.

In this contribution, we present a summary of our current database of serpentine affinity in the California flora. The database was constructed via an extensive literature search, expert opinion, field observations, web research, and intensive use of accession records at key herbaria. It provides data on levels of serpentine endemism, rarity, geographic distribution, taxonomy, and lifeform.

METHODOLOGY

We began by conducting a database search of the electronic Jepson Manual (Hickman 1993) maintained by the Jepson Herbarium at the University of California-Berkeley (UC-JEPS 2004a). The database was queried for all taxa with "serpentine", "ultramafic", or related (e.g., "asbestos soils") references in the habitat description. Taxa containing "non-serpentine" in the description were removed afterward. We cross-checked the 391 serpentine-related taxa found in the Jepson Manual with Kruckeberg (1984), who listed those taxa he believed to be endemic to ultramafic substrates in California, and those that were either local or regional "serpentine indicators" (i.e., nonendemic taxa whose distributions are nonetheless skewed toward occurrences on ultramafics). Taxonomic updates in the Jepson Manual (Hickman 1993) were applied to the Kruckeberg list (which included 377 taxa after these revisions), and then those taxa not on the Jepson-derived list were added to our database. This resulted in a list of 529 taxa; of these, 287 were not shared between the two sources. We then added to the list a number of taxa that we considered to be likely endemics or indicators but which were not indicated as such by either Kruckeberg (1984) or the Jepson Manual (1993). Finally, published literature (e.g., Meinke and Zika 1992; Nelson and Nelson 2004; Baldwin 1999 and 2001; Barkley 1999; Porter and Johnson 2000; Zika et al. 1998) and the online Jepson Interchange Jepson Flora Project (UC-JEPS 2004b) were consulted for taxonomic revisions and taxa newly described since the publication of the Jepson Manual.

To score the affinity of taxa to ultramafic substrates, we adopted a modification of Kruckeberg's measures of ultramafic "fidelity". In his Appendix C, Kruckeberg (1984) used two or three "+"s to signify increasing levels of endemism: three "+"s were attached to taxa with 95–100% of their occurrences found on ultramafics, two "+"s signified taxa with 85–94% fidelity. In his Appendix D, Kruckeberg used one or two exclamation marks ("!"s) to signify increasing levels of fidelity to ultramafic substrates among supposed nonendemic "indicator" taxa. In both appendices, question

marks ("??") were attached to those taxa for which more information was necessary to confidently assign their status. Some of the "tentative" endemics were included in the indicator appendix as well, thus these taxa occur twice in Kruckeberg's lists. We combined Kruckeberg's two scales, and added two levels to yield six levels of ultramafic affinity, where 6 represents a "strict endemic" ($\geq 95\%$ of occurrences on ultramafics), and successively lower values signify lower affinity to the substrate (5 = 85–94% of occurrences; 4 = 75–84%; 3 = 65–74%; 2 = 55–64%; 1 = 45–54%). By this definition, "1" thus represents a species found about half of the time on serpentine. We consider scores between 1 and 2 to indicate "weak indicators", and a score of about 1 to mean an "indifferent" taxon. The Kruckeberg fidelity scale crosswalks to ours in the following fashion: "+++" = 6; "++" = 5; "!!" = 3; one "!" = 2. Those taxa which occurred in both Kruckeberg's endemic and indicator tables had their two scores averaged: these all fell between "3" and "4" on our scale. For example, *Cupressus macnabiana* was rated "+++" in Kruckeberg's Appendix C (i.e., "6" on our scale), and "!!" [i.e., "2" in our scale] in Appendix D; these were averaged to "4" on our scale.

We attached our categorical levels of ultramafic affinity to all of the species in our hybrid Jepson-Kruckeberg database. In the case of the Kruckeberg taxa, we simply cross-walked the Kruckeberg fidelity codes to our scale as described above, making some adjustments based on more recent taxonomic revisions and combinations. In the case of the Jepson Manual taxa, we were forced to interpret the language used in habitat descriptions to determine levels of affinity. We used the following interpretations of description language to assign affinities: a "6" was assigned where the habitat description categorically stated "serpentine" or "ultramafic" (a "5" if there was some indication that this restriction was not absolute); a "4" was assigned where the modifiers "generally" or "usually serpentine" were used; "especially" or "often" equaled "3"; "sometimes" or "occasionally" equaled "1". In a few cases, affinity levels were assigned based on ancillary information in the habitat and/or range description rather than on explicit statement of serpentine affinity.

We then conducted a broad survey of the literature, regional botanical experts, and herbaria records to obtain as many sources as possible for each taxon in our database, and to add to the database any taxa we might have overlooked. We manually consulted every species description in a variety of regional and local floras (Clifton 2001; Ertter and Bowerman 2004; Howell 1970; McMinn 1939; Oswald 2002; Smith and Wheeler 1992), and guidebooks to rare and sensitive taxa (Hanson 1999; Hoover et al. 1993; Jimerson et al. 1995; McCarten 1988; McCarten and Rogers 1991; Nakamura and Nelson 2001; Trinity SIPS 2001; USFWS 1998).

We also consulted the CalFlora Online Species Database (CalFlora 2004), and the California Native Plant Society Online Inventory of Rare and Endangered Plants (CNPS 2004). We added columns to our database for each source, and gave scores (1–6, as described above) to each taxon for which a habitat description suggested an ultramafic affinity. Information on serpentine affinity in the CalFlora database is limited to taxa from the Sierra Nevada and to rare taxa statewide, and does not include sufficient information to determine degree of affinity (A. Dennis, personal communication). CalFlora was therefore not treated as a typical “source”, and CalFlora serpentine taxa were simply given a score of 0.5 to be added later to the sum of scores when final ultramafic affinities were calculated (see below). The California Natural Diversity Database (CNDDB) was not searched, as we consulted all of the primary resources originally used to build CNDDB, and the CNPS Online Inventory (see above) is updated from the same contemporary sources as CNDDB.

We calculated preliminary mean affinities for taxa in our database by summing the scores across source columns and adding the CalFlora score (if present), then dividing by the number of sources (not including CalFlora) for the taxon in question. We also calculated the number of sources, the median score, and the standard deviation and standard error of the scores for each taxon. We then sent the database to approximately 40 state and regional experts for their review and input, and asked them to score serpentine affinity using the 1–6 scale for taxa with which they were familiar. These individuals included botanists employed by federal and state land management agencies, universities, museums, non-governmental organizations, and private consulting firms. We received 17 substantive replies, and incorporated their input into an updated database.

The next step was to ensure that we had at least three sources of serpentine affinity for each taxon in our database; given the great differences between the Jepson Manual and Kruckeberg’s list, we felt a third opinion was important. We focused on those taxa for which we had less than three sources, as well as those with high variability in scores. We began by consulting the habitat descriptions in Munz and Keck (1968) for every taxon in our database with less than three sources. We then turned to Herbaria accession records. We searched the online “SMASCH” accession databases of the UC and Jepson Herbariums at UC-Berkeley at (UC-JEPS 2004c) for all taxa with one or two sources, and for all taxa with affinity-score standard deviations ≥ 1.0 (a total of 548 taxa). For any Northern California taxa remaining with less than three sources and/or high variability, we then searched the online accession database of the Biological Sciences Herbarium at Chico State University (CSU-BSH 2004; a total of 164 taxa were searched).

In our online accession database research, we followed the following protocol:

1. We began with the most recent accession records and worked backwards, as habitat descriptions before the mid 1970’s usually lack sufficiently detailed information on substrate and location.

2. We consulted the habitat description for each record. If the description included enough information to determine the substrate, we noted whether it was ultramafic or non-ultramafic. We did not count multiple accession records from the same collecting trip and location as different records.

3. On the average, about $\frac{1}{3}$ of the accession records consulted had sufficient information to determine if a collection had been made on ultramafics or not. Not all of these determinations were made simply based on the collector’s habitat description. For example, many California counties do not contain outcrops of ultramafic rocks (e.g., Los Angeles, San Diego, San Bernardino, Modoc). Collections from these counties were coded as “nonserpentine” even where habitat descriptions were missing. Also, collections from well-known collecting locations on ultramafics (e.g., Blue Banks in Glenn County, Red Butte in Siskiyou County, or the mouth of 18-Mile Creek on the Middle Fork Smith River, Del Norte County) were coded as “serpentine” even where habitat descriptions were missing. Finally, where we had trouble getting a sufficient number of records with habitat descriptions, or where it was otherwise critical to get more information, we used location information in the accession record (where it existed) to do further research. We used TOPO! Software (National Geographic Maps 2000) to locate coordinates or named locations and then consulted geological maps (ranging from 1:250,000 to 1:25,000) to determine if the location was on an ultramafic outcrop. Only those occurrences which could be confidently assigned to ultramafics were identified as such.

4. We continued until we had recorded habitat information from at least 10% of the total accession records for the species in question. Our minimum was 10 records, unless there were fewer than 10 records with habitat descriptions and reasonably locatable site information (286/548 taxa had fewer than 10). Our maximum was usually 20, although we went beyond 20 in some cases.

5. We summarized the accession record results for each taxon by dividing the total number of records with sufficient habitat or location information to determine substrate by the number of records recording serpentine/ultramafics, and then multiplied the result by 100 to get a percentage. We then cross-walked the percent value to our scale of ultramafic affinity: 95–100% of records on ultramafics = 6; 85–94% = 5; 75–84% = 4; 65–74% = 3; 55–64% = 2; 45–54% = 1; 35–44% = 0.75; 25–34% = 0.5; 15–24% = 0.25; >0–14% = 0.1; 0 = 0.

Finally, T. Nelson and S. Carothers also used the

Humboldt State University Herbarium to provide information to us on a number of under-documented taxa from Northwestern California.

In our accession records research, we necessarily assumed that: (1) the taxon itself was correctly identified on the accession record; (2) the substrate was correctly identified by the collector; and (3) ultramafic substrates were neither more nor less likely to be identified correctly (or at all) than other substrates. The last assumption is probably flawed, as serpentine and other “charismatic” substrates—given their close connection to plant endemic taxa and their relative ease of identification—are almost certainly more likely to be identified than “normal” substrates. This could theoretically lead to accession records “overstating” the degree of a taxon’s affinity to ultramafic substrates. In practice, however, we found that the accession records were generally somewhat more conservative than our literature sources vis-à-vis the serpentine affinities of the taxa in our database.

Our final database included 18 columns of information sources for serpentine affinity, plus a column for CalFlora. We summed these affinity values and took their mean (not including CalFlora in the denominator). We also calculated the mean without CalFlora, the median, the standard deviation, and the standard error. We identified each taxon by taxonomic category (pteridophyte, gymnosperm, dicot or monocot), and by lifeform (annual forb, perennial forb, annual graminoid, perennial graminoid, shrub, tree). For rare taxa, we added the rarity rating from the California Native Plant Society Online Database of Rare and Endangered Plants (version 6.04d, 11-12-2004). The following information was also added to the complete database: geographic distribution in California for each taxon (by Jepson Manual geographic subdivisions); elevational range (from Hickman 1993); the geographic distribution of, and number of species of the genus of each taxon (from Mabberly 1996); and the common name (from Hickman 1993, and the Natural Resource Conservation Service PLANTS online database [USDA-NRCS 2005]). Aside from a summary of the geographic distribution, this information is not presented in the current paper, but is available on request from the first author, as are the affinity values calculated for each source.

RESULTS

A summary table of the current database is presented in Appendix 1. Appendix 1 includes 669 taxa, ranging in affinity from 6.25 to 1.00 (some values exceed 6 because they were identified as serpentine taxa in the CalFlora Database). Our full database includes 698 taxa, 29 of which have mean serpentine affinities of < 1 ; we did not include these taxa in the current paper. The greatest number of sources we located for any single taxon was nine (four taxa). We found eight sources for eight taxa

and seven sources for 19 taxa; 587 taxa had between three and six sources. Eighty-one taxa had fewer than three sources (77 with two, three with one). Somewhat more than half of the taxa (387) in our original list had standard deviations for serpentine affinities > 1.0 .

Since our serpentine affinities are calculated as the means of multiple sources, our values fall on a continuous scale, rather than in categories. Given this, we recognized taxa with mean affinities > 5.5 as “strict endemics” (analogous to Kruckeberg’s “+++”, or taxa with $> 95\%$ of their occurrences on ultramafics), and taxa with mean affinities > 4.5 and < 5.5 as “broad endemics” (analogous to Kruckeberg’s “++”, taxa with about 85–94% of their occurrences on ultramafics). Using these definitions, 164 taxa are strict endemics, while 82 taxa are broad endemics, for a total of 246 endemic taxa; 176 of these are full species. Among the remaining taxa, 123 are “strong serpentine indicators” (Kruckeberg 1984), with scores ranging from 2.5 to 3.4 (about 65–74% of their occurrences on ultramafics); 150 are “weak indicators”, falling between 1.5 and 2.4 on our scale (± 55 –64% of their occurrences on ultramafics); and 79 fall in a gray area between weak indicators and indifferent taxa (between 1.0 and 1.4 on our scale, or about 50–54% of occurrences). Seventy-one taxa have affinity scores between 3.5 and 4.4 (about 75–84% of their occurrences on ultramafics), and thus represent the transition from strong indicators to broad endemics.

Six families account for more than half of all the endemics: Asteraceae, Liliaceae, Brassicaceae, Polygonaceae, Scrophulariaceae, and Apiaceae (Table 1). The 20 most important plant families among the serpentine endemics are shown in Fig. 1, with the percentage of the serpentine endemic flora that they contribute, as well as the percentage of the total California endemic flora that they contribute. Families that proportionally contribute more to the serpentine endemic flora than to the California endemic flora include Liliaceae, Brassicaceae, Polygonaceae, Linaceae and Caryophyllaceae. Families whose level of endemism is much lower on serpentine than it is statewide include Fabaceae, Poaceae, Boraginaceae, and Rosaceae (Fig. 1).

The most diverse genera in our list of serpentine endemics are *Streptanthus* (Brassicaceae) and *Eriogonum* (Polygonaceae), followed by *Hesperolimon* (Linaceae) and *Arctostaphylos* (Ericaceae) (Table 2). There are 21 genera with at least four taxa among the endemics. These represent 14 plant families, with Asteraceae (four genera among the endemics), Liliaceae (three genera), Scrophulariaceae (two genera) and Brassicaceae (two genera) the only families with multiple genera in the list. Figure 2 compares the contribution of these genera to the serpentine endemic flora with their contribution to the California endemic flora. All but five or six of these genera have a greater level of endemism to serpentine than they have within the State as a

TABLE 1. NUMBERS OF SERPENTINE ENDEMIC AND NEAR ENDEMIC TAXA, BY FAMILY. ¹ Strict endemics. ² Strict endemics plus broad endemics. ³ Strict and broad endemics plus "near endemic" taxa (taxa transitional from strong indicators to broad endemics).

| Family | Serpentine affinity score | | | Total taxa |
|------------------|---------------------------|-------------------|-------------------|------------|
| | ≥5.5 ¹ | ≥4.5 ² | ≥3.5 ³ | |
| Asteraceae | 26 | 37 | 45 | 106 |
| Liliaceae | 15 | 28 | 37 | 85 |
| Brassicaceae | 21 | 26 | 31 | 46 |
| Polygonaceae | 10 | 17 | 19 | 39 |
| Scrophulariaceae | 9 | 14 | 18 | 37 |
| Apiaceae | 7 | 10 | 13 | 32 |
| Linaceae | 8 | 9 | 9 | 14 |
| Ericaceae | 5 | 8 | 10 | 15 |
| Polemoniaceae | 6 | 7 | 8 | 18 |
| Caryophyllaceae | 5 | 7 | 8 | 18 |
| Fabaceae | 4 | 7 | 10 | 24 |
| Lamiaceae | 4 | 6 | 10 | 17 |
| Crassulaceae | 5 | 5 | 7 | 13 |
| Rhamnaceae | 4 | 5 | 6 | 14 |
| Campanulaceae | 3 | 5 | 8 | 12 |
| Onagraceae | 3 | 5 | 7 | 12 |
| Hydrophyllaceae | 4 | 4 | 8 | 15 |
| Rubiaceae | 3 | 4 | 4 | 8 |
| Convolvulaceae | 1 | 4 | 5 | 6 |
| Cyperaceae | 1 | 4 | 5 | 8 |
| Poaceae | 1 | 3 | 3 | 19 |
| Portulacaceae | 0 | 3 | 5 | 16 |
| Boraginaceae | 2 | 2 | 3 | 10 |
| Gentianaceae | 2 | 2 | 2 | 3 |
| Iridaceae | 2 | 2 | 2 | 4 |
| Malvaceae | 2 | 2 | 2 | 5 |
| Salicaceae | 2 | 2 | 2 | 3 |
| Garryaceae | 1 | 2 | 2 | 2 |
| Rosaceae | 1 | 2 | 5 | 10 |
| Cupressaceae | 0 | 2 | 3 | 6 |
| Violaceae | 0 | 2 | 3 | 7 |
| Asclepiadaceae | 1 | 1 | 1 | 1 |
| Berberidaceae | 1 | 1 | 1 | 4 |
| Dryopteridaceae | 1 | 1 | 1 | 2 |
| Fagaceae | 1 | 1 | 1 | 3 |
| Lentibulariaceae | 1 | 1 | 1 | 1 |
| Papaveraceae | 1 | 1 | 1 | 5 |
| Ranunculaceae | 1 | 1 | 3 | 6 |
| Orchidaceae | 0 | 1 | 1 | 3 |
| Pteridaceae | 0 | 1 | 1 | 4 |
| Verbenaceae | 0 | 1 | 1 | 1 |
| Cistaceae | 0 | 0 | 0 | 1 |
| Orobanchaceae | 0 | 0 | 0 | 1 |
| Pinaceae | 0 | 0 | 1 | 6 |
| Plantaginaceae | 0 | 0 | 0 | 1 |
| Polygalaceae | 0 | 0 | 0 | 1 |
| Primulaceae | 0 | 0 | 0 | 1 |
| Sarracenaceae | 0 | 0 | 1 | 1 |
| Saxifragaceae | 0 | 0 | 1 | 2 |
| Sterculiaceae | 0 | 0 | 0 | 1 |
| Totals | 164 | 246 | 315 | 669 |

whole. These genera include *Streptanthus*, *Hesperolinon*, *Lomatium* and *Minuartia*. Only one genus (*Phacelia*) contributes less to the serpentine endemic flora than it does to the State as a whole; *Arc-*

tostaphylos contributes a similar percentage to both floras (Fig. 2).

Of the taxa in our database, there are 532 dicots (of which 204 are endemic), 119 monocots (38 endemics), 12 gymnosperms (2 endemics) and six pteridophytes (2 endemics). 207 taxa are annual forbs (of which 71 are endemics, including 7 of 14 that can also be perennial/biennial), 383 are perennial forbs (150 endemics, including the 7 "annuals" and 6 taxa which can also be shrubs), 24 are perennial graminoids (7 endemics), 64 are shrubs (23 endemics, including 6 taxa shared with the perennial forbs and 1 which assumes both tree and shrub forms), and 12 are trees (2 endemics) (Appendix 1). Of the endemic perennial forbs, 24 are bulb plants (all Liliaceae), 17 are rhizomatous (from ten different Families), three are hemiparasites (Scrophulariaceae), and one is carnivorous (Lentibulariaceae) (Appendix 1).

Using Kruckeberg's (1984) physiographic provinces of California (which correspond more or less to major geographic subdivisions mapped in the Jepson Manual (Hickman 1993)), we found the following geographic distribution of serpentine endemic taxa (Fig. 3): The North Coast, considered *in toto* (i.e., the Jepson Manual's NCo and NCoR subregions (Hickman 1993)), supports approximately 118 serpentine endemics, with 49 of these restricted to that area. The Klamath Region (Jepson Manual subregion KR), supports 98 endemic taxa, with 54 restricted to that area (including taxa also found in neighboring SW Oregon). The San Francisco Bay Area (Jepson Manual subregion SnFrB plus the sections of NCo and CCo bordering it) supports about 51 endemics, with 24 found only there. The South Coast Ranges, including the Channel Islands and the Santa Ana Mountains (i.e., Jepson Manual subregions CCo, SCoR plus the few ultramafic outcrops that occur in the Jepson SW Region), support 43 total endemics with 24 restricted to that area. The Sierra Nevada (Jepson Manual region SN) support 38 total serpentine endemic taxa, with 21 taxa restricted to the Range (Fig. 3).

Of the 669 taxa in our database, 295 are listed as "rare" or "uncommon" by the California Native Plant Society (CNPS) (Appendix 1). These include 194 of the 246 taxa that we consider to be either strict or broad serpentine endemics. One serpentine endemic taxon, *Arctostaphylos hookeri* subsp. *franciscana*, is extinct in the wild and survives only in cultivation. Of the 295 rare or uncommon taxa, 154 are on CNPS List 1b, which lists plants considered threatened or endangered by either the State or Federal governments, as well as unlisted plants which CNPS considers rare enough to warrant listing; 111 of these List 1b plants are serpentine endemics by our definition. Nine taxa (seven endemics) from Appendix 1 are on CNPS list 2, which contains plant taxa that are rare in California but are not restricted completely to the State; all of these taxa are either State listed and threatened or endangered,

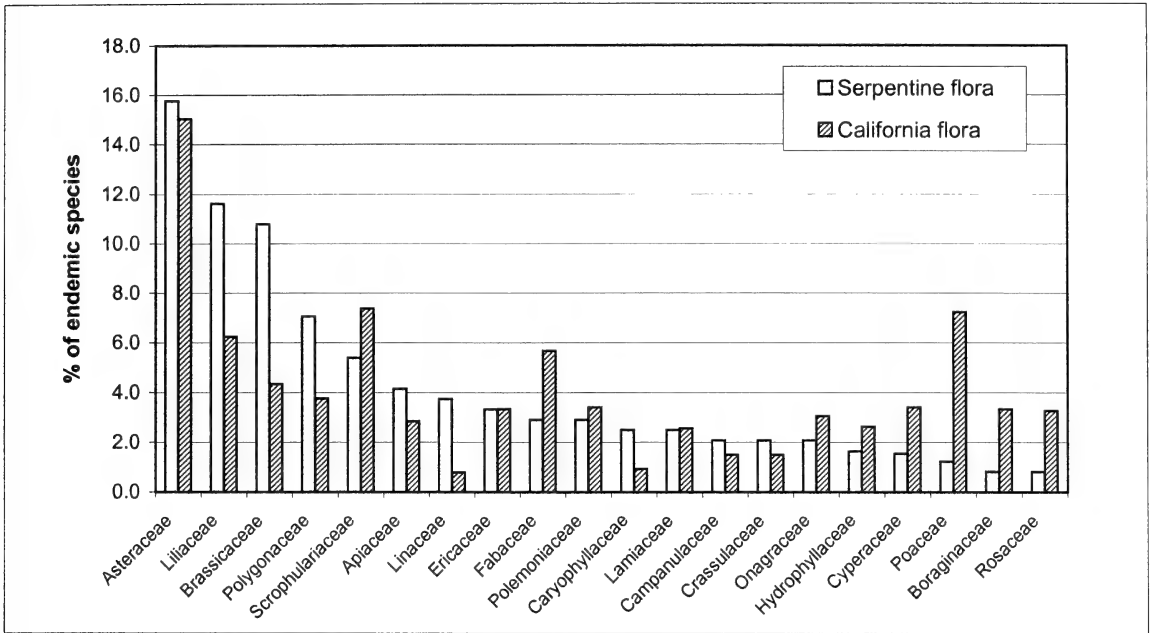


FIG. 1. The twenty most important plant families of serpentine endemic plants (i.e., including strict and broad serpentine endemics), with the percentage of endemic species they contribute to the serpentine endemic flora in California, and to the California endemic flora as a whole.

or are eligible for listing. Eight taxa (four endemics) in Appendix 1 are found on CNPS list 3, which lists uncommon taxa for which more information is required. Of taxa in Appendix 1, 123 (71 endemics) are on CNPS list 4, which contains taxa of “limited distribution or infrequent throughout a broader area in California”.

TABLE 2. GENERA WITH MORE THAN THREE TAXA ENDEMIC TO SERPENTINE.

| Genus | Family | Endemic taxa |
|--------------------------|------------------|--------------|
| <i>Streptanthus</i> | Brassicaceae | 18 |
| <i>Eriogonum</i> | Polygonaceae | 14 |
| <i>Hesperolinon</i> | Linaceae | 9 |
| <i>Arctostaphylos</i> | Ericaceae | 8 |
| <i>Allium</i> | Liliaceae | 7 |
| <i>Lomatium</i> | Apiaceae | 7 |
| <i>Packera (Senecio)</i> | Asteraceae | 6 |
| <i>Calochortus</i> | Liliaceae | 5 |
| <i>Cordylanthus</i> | Scrophulariaceae | 5 |
| <i>Arabis</i> | Brassicaceae | 4 |
| <i>Calystegia</i> | Convolvulaceae | 4 |
| <i>Carex</i> | Cyperaceae | 4 |
| <i>Castilleja</i> | Scrophulariaceae | 4 |
| <i>Cirsium</i> | Asteraceae | 4 |
| <i>Erigeron</i> | Asteraceae | 4 |
| <i>Fritillaria</i> | Liliaceae | 4 |
| <i>Galium</i> | Rubiaceae | 4 |
| <i>Lessingia</i> | Asteraceae | 4 |
| <i>Minuartia</i> | Caryophyllaceae | 4 |
| <i>Monardella</i> | Lamiaceae | 4 |
| <i>Phacelia</i> | Hydrophyllaceae | 4 |

DISCUSSION

In 1984, Kruckeberg estimated that the serpentine endemic flora of California numbered approximately 220 taxa (about 180 full species), and that a further 230 taxa were sufficiently associated with ultramafics to be “indicators” of the substrate. Thus, Kruckeberg believed that about 450 taxa were associated with serpentine in California. Although our results suggest that the number of serpentine-associated taxa is closer to 670, they also suggest that Kruckeberg’s (1984) estimate of the number of full-species endemics was remarkably accurate (180 vs. 176). As Kruckeberg’s numbers also suggested, serpentine endemics therefore comprise approximately 12.5% (176/1410) of the plant species endemic to California. Based on numbers from the Jepson Manual (Hickman 1993; R. Moe personal communication), the percentage of serpentine endemics among California endemic species, subspecies and varieties is about 11.4% (246/2153).

Kruckeberg’s (1984) estimates of endemics by California geographic region are somewhat less accurate than his statewide estimate (see Fig. 3), but Kruckeberg’s data sources in the 1970’s and early 1980’s were extremely limited compared to ours. As did Kruckeberg, we found that the North Coast Ranges support more serpentine endemics plants than any other geographic region, but that the Klamath Ranges (and adjoining SW Oregon) support many more restricted endemics than Kruckeberg thought was the case (54 vs. 30). Kruckeberg’s estimates for the numbers of restricted endemics in

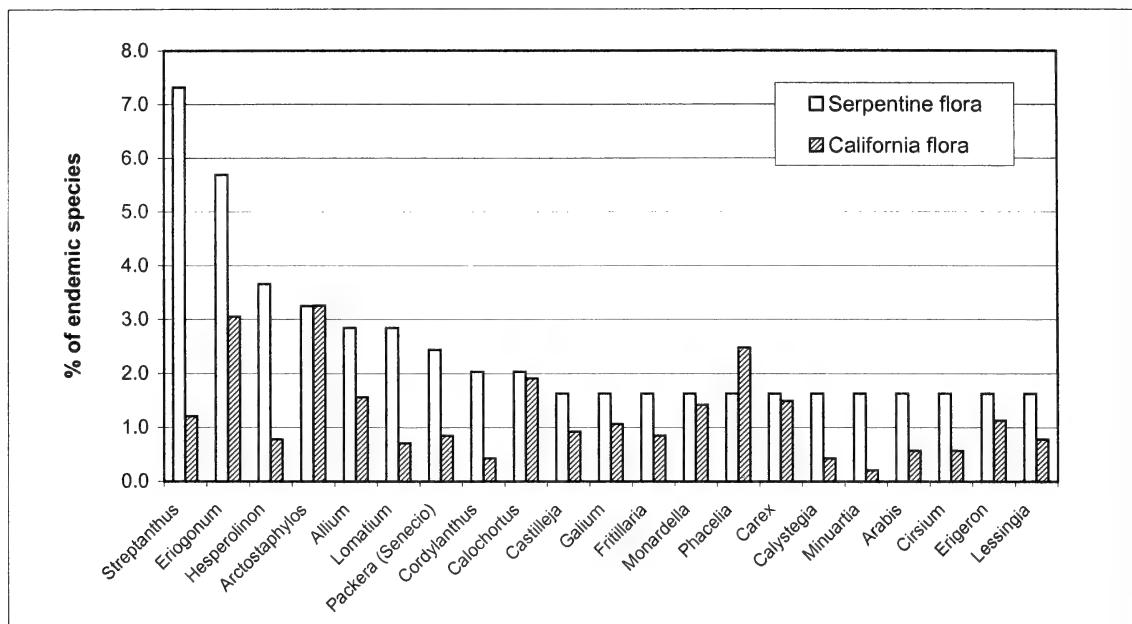


FIG. 2. The twenty-one most important genera of serpentine endemic plants (i.e., including strict and broad serpentine endemics), with the percentage of endemic species they contribute to the serpentine endemic flora in California, and to the California endemic flora as a whole.

the North Coast Ranges and the Bay Area are very similar to our numbers (Fig. 3), but he overestimated the number of endemics in the South Coast Ranges (36 vs. 24). Kruckeberg estimated that either 13 or 16 (depending on whether one goes by the text or the tables in Appendix E) endemic taxa were restricted to the Sierra Nevada; we found 21 taxa thus restricted.

Reasons for differences between our numbers and Kruckeberg's (1984) are many, but belong to two broad categories. The primary reason is quality and quantity of information. In many cases, Kruckeberg's information had to come through his own field experience, or through hard copy herbarium records, which—before the late 1970's—were no-

toriously uninformative when it came to habitat description. In contrast, many data sources we accessed were available electronically and could be queried and retrieved remotely.

The other principal reason for difference is the inevitable discoveries and taxonomic reorganizations that occur over a 20-year period. Kruckeberg's work came before publication of the Jepson Manual (Hickman 1993), which contained many significant changes in California plant taxonomy. A considerable number of serpentine endemic taxa in the Jepson Manual were wholly unknown to Kruckeberg in 1984. Examples include *Calochortus raichei* S. Farwig & V. Girard, *Minuartia stolonifera* T. W. Nelson & J. P. Nelson, *Perideridia bacigalupii* Chuang & Constance, and *Monardella stebbinsii* Hardham & J. Bartel. Since the Manual's publication, there have been further changes (e.g., Barkley 1999; Baldwin 1999; Porter and Johnson 2000). Serpentine endemic taxa named since publication of the Jepson Manual include *Harmonia guggolziorum* B. G. Baldwin, *Carex serpentinicola* P. F. Zika, and *Silene serpentinicola* T. W. Nelson & J. P. Nelson.

As a null hypothesis, one might expect that the distribution of endemic plant taxa across plant families and genera on California serpentes would more or less mirror the distribution of endemics in the State as a whole. Our data demonstrate that this assumption is incorrect at both taxonomic levels, but the root of this difference seems to be largely at the level of genus. A number of families contribute a much higher proportion of the serpentine

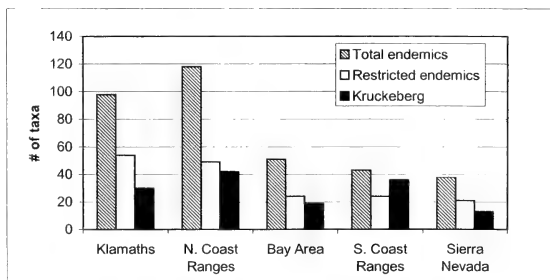


FIG. 3. Geographic distribution of serpentine endemic taxa in California. "Total endemics" includes all California serpentine endemic taxa present in a given region; "restricted endemics" includes only those taxa restricted to a given region; black bars represent Kruckeberg's (1984) estimates of restricted endemics.

TABLE 3. EXAMPLES OF “REGIONAL” SERPENTINE INDICATORS, *SENSU* KRUCKEBERG (1984). ¹ CA = California, KL = Klamath Ranges, NC = North Coast Ranges, BA = San Francisco Bay Area, SC = South Coast Ranges, SN = Sierra Nevada.

| Taxon | Distribution ¹ | Comments ¹ |
|---|---------------------------|---|
| <i>Allium amplexans</i> | CA | SC—broad endemic; Northern CA—weak indicator at best |
| <i>Aspidotis densa</i> | CA | Marin County—broad endemic; rest of NC—weak to strong indicator; KL—broad endemic to strong indicator, depending on locality; rest of CA—strong indicator |
| <i>Festuca californica</i> | CA | Northern SN and KL—strong indicator to broad endemic; NC—primarily weak indicator; rest of CA—indifferent |
| <i>Lupinus onustus</i> | KL, SN | KL—broad endemic; SN—indifferent (mostly non-ultramafic) |
| <i>Pinus attenuata</i> | CA | Mendocino County and neighboring NC—broad endemic; rest of NC and SC—strong indicator; KL—weak indicator; SN—weak indicator to indifferent |
| <i>Pinus jeffreyi</i> | KL, NC, SC, SN | KL and NC—± strict endemic; Westslope of northern SN—strong indicator; rest of CA—indifferent |
| <i>Quercus vaccinifolia</i> | KL, NC, SN | Mendocino County and neighboring NC—broad endemic; Northern NC and KL—weak indicator; SN—indifferent |
| <i>Sedum obtusatum</i> ssp. <i>obtusatum</i> | KL, SN | KL and NC—± broad endemic; SN—weak indicator or indifferent |
| <i>Stachys pycnantha</i> | CA | Marin County—broad endemic to strong indicator; Northern SN—very weak indicator; rest of CA—weak indicator or indifferent |
| <i>Viola douglasii</i> | CA | Plumas County—endemic; NC—strong indicator; rest of CA—indifferent |

endemic flora than they do of the California endemic flora (Fig. 1), but our database shows that most of these “anomalies” are due to one or two genera within those families (see Fig. 2). Examples include *Fritillaria* and *Allium* in Liliaceae, *Minuartia* in Caryophyllaceae, *Streptanthus* and *Arabis* in Brassicaceae, *Hesperolinon* in Linaceae, and *Eriogonum* in Polygonaceae. Many of these genera are well-known as foci of neoendemism (i.e., genera with groups of actively and rapidly speciating taxa) (Raven and Axelrod 1978). It is interesting that such prominent California plant families like Scrophulariaceae, Hydrophyllaceae, Boraginaceae, Onagraceae and Polemoniaceae are underrepresented on serpentine substrates. Certain highly diverse genera in California are also proportionally underrepresented as serpentine endemics (e.g., *Clarkia*, *Phacelia*, *Ceanothus*, *Gilia*, and *Mimulus*).

As we constructed our database, taxa with high variability in serpentine affinity scores were tagged for further research (e.g., through accession records; see Methodology) so that we might be able to discern taxa that truly varied geographically in their affinities from taxa that simply suffered from inadequate or faulty information. The former were called “regional indicators” by Kruckeberg (1984), i.e., taxa that are considered serpentine endemics or indicators in one part of their range but show less or no affinity for ultramafic substrates in other parts of their range. In his Appendix D, Kruckeberg (1984) tried to summarize where the different regional indicators he had identified occurred on ultramafics. We refer the reader to Kruckeberg (1984) for details on these taxa (most of which also occur in our database), but most regional indicators in our database can be recognized by searching for taxa with: (1) relatively wide geographic distributions,

(2) lower mean serpentine affinity scores, and (3) high standard deviations in their affinity scores. Table 3 lists ten examples of regional indicator taxa in our database.

Some of the variability in our serpentine affinity scores is thus due to geographic variation in affinities, but some is also due to inadequate, statistically biased, or even faulty information from our sources. We attempted to offset these sources of variability by including as many sources as possible in our database (and by using accession records), but were not successful in all cases. We consider any taxon with a standard deviation in affinity score > 1.5, or having fewer than three sources, as being in “need of further research”; this includes about a third of the taxa in our database. Examples of such taxa include: *Lupinus lapidicola*—called a strict serpentine endemic by Kruckeberg (1984) and a strong serpentine indicator by CNPS (2004), and with 2/2 accession records in SMASCH with ultramafic habitat descriptions, but stated as occurring only on granites by the Jepson Manual (Hickman 1993) and Munz and Keck (1973); *Phacelia phacelioides*—Kruckeberg (1984) and V. Yadon (personal communication) believe this is a strict endemic, but the Jepson Manual is mute on the subject, and only 1/3 accession records in SMASCH are on ultramafics (but the two nonserpentine locations may have misidentified geology given the location); and *Allium lacunosum* var. *lacunosum*—both the Jepson Manual and Kruckeberg rate this as a strict endemic, Munz and Keck score it a strong indicator, but SMASCH has only 1/6 records on ultramafics.

Some species had surprising levels of ultramafic affinity. For example, our database includes a number of taxa that we personally have only rarely seen

on serpentine (e.g., *Lathyrus vestitus* var. *vestitus*, *Apiastrum angustifolium*, *Emmenanthe penduliflora* var. *penduliflora*). It also includes other taxa which we would have characterized as being clearly indifferent to ultramafic substrates, but which scored higher based on our sources (e.g., *Adenostoma fasciculatum*, *Pinus balfouriana* ssp. *balfouriana*). As noted above, some of these “discrepancies” may be due to inadequate or biased data—the ultramafic affinity of these types of taxa will drop as we collect more information. Many of these surprising affinities are probably real however, and they are simply a sign of our limited knowledge of the relationships between California plant life and ultramafic substrates.

In accession records, and in the literature, botanists and ecologists frequently misidentified basic rock types. For example, in accession records we found a number of examples of peridotite being called “volcanics” or even “sandstones”. We also found multiple examples, in accession records as well as in the literature, of gabbro and other basic intrusive rocks being misidentified as ultramafics. Gabbro and “basic” rocks are “mafic” in composition—that is to say, they usually contain visible feldspars and they are geochemically distinct from ultramafic rocks. For example, the average alkali-gabbro contains 4–5 times as much Na as peridotite, 5–10 times as much P, 3–4 times as much K and Ca, and about ½ as much Mg (Ehlers and Blatt 1982). The famous gabbro outcrops of Eldorado County (Pine Hill) or San Diego County are therefore *not* ultramafic, even though the effect of the substrate on plant physiognomy and community composition may appear similar. A number of species in our database appear to be primarily, if not exclusively gabbro endemics, but we lacked sufficient information to remove them from our list. These include *Acanthomintha ilicifolia*, *Fremontodendron californicum* ssp. *decumbens*, and *Calochortus weedii* var. *vestus*.

As has been frequently noted (Mason 1946a, b; Raven and Axelrod 1978; Kruckeberg 1984, 2002; Skinner and Pavlik 1994; McCarten 1997), California’s ultramafic soils support a very high proportion of the State’s rare plants. Based on our database, almost 11% (111/1021) of California’s rare plant taxa are either broadly or strictly restricted to ultramafic substrates; 15% of List 1b taxa (154/1021) show high affinity for ultramafic substrates (i.e., they are endemics or indicators). In northwestern California, 15% of plant taxa managed as “sensitive” by the Forest Service are serpentine endemics, and fully 30% are closely associated with ultramafics (J. K. Nelson and L. Hoover personal communication). In 2002, Kruckeberg wrote that “preservation of serpentine habitats in California is spotty, inadequate, and largely coincidental”. Given the great importance of ultramafic substrates to the richness and distinctiveness of the California flora, the conservation of these unique habitats

should be a high priority for land management agencies and private conservation organizations throughout the State.

Our database of serpentine affinity updates, and expands on the widely-used tables of serpentine endemic and “indicator” taxa published in 1984 by Art Kruckeberg in his classic monograph on California serpentine ecology. Our data are also a quantitative synthesis of the qualitative (and usually incomplete) allusions to serpentine affinity contained in habitat descriptions in California floras and flora databases, including Munz and Keck (1973), Hickman (1993), Oswald (2002), the online CalFlora Database (CalFlora 2004), and the California Native Plant Society Online Inventory of Rare and Endangered Plants (CNPS 2004). Our data on serpentine endemism should prove valuable to efforts in ecology, biosystematics (Baldwin 1995), conservation, and land management. In particular, we hope that our database will help us better understand the nature and degree of serpentine endemism in the California flora, and we hope it will spur the collection of additional, critical information necessary for conserving the rare plants and habitats of ultramafic substrates.

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APPENDIX 1. PLANT TAXA WITH HIGH AFFINITY TO ULTRAMAFIC SUBSTRATES IN CALIFORNIA. Ordered by family and taxon. ¹ Names as in Hickman (1993); names in parentheses are based on more recent revisions (see text for sources). ² Affinity: SE = weak indicator/indifferent. ³ Mean affinity score, including information from CalFlora. ⁴ Sum of all affinity scores, including CalFlora. ⁵ Median of affinity scores. ⁶ Standard deviation of affinity scores. ⁷ Standard error of affinity scores. ⁸ California Native Plant Society rarity codes, from CNPS Inventory of Rare and Endangered Plants of California, 11-2004. ⁹ Geographic distribution: KL = Klamath Ranges, NC = North Coast Ranges, BA = San Francisco Bay Area, SC = South Coast Ranges, SN = Sierra Nevada. ¹⁰ Taxonomic category. ¹¹ carn = carnivorous, cesp = caespitose, hemipar = hemiparasitic, paras = parasitic, rhiz = rhizomatous. See text for more information.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|--|--|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|-------|----------------|-------------------------|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | |
| <i>Angelica tomentosa</i> <i>Aptastrum angustifolium</i> <i>Ligusticum californicum</i> <i>Lomatium ciliolatum</i> <i>Lomatium congdonii</i> <i>Lomatium dasycarpum</i> ssp. <i>dasycarpum</i> | Apiaceae | SI | 2.7 | 8 | 3 | 3.0 | 1.5 | 0.9 | | 1 | 1 | | 1 | Dicot | Perennial forb | |
| | Apiaceae | WI | 1.5 | 7.6 | 5 | 0.1 | 2.5 | 1.1 | | 1 | 1 | 1 | | Dicot | Annual forb | |
| | Apiaceae | WI/IN | 1.4 | 5.75 | 4 | 1.4 | 1.3 | 0.7 | | 1 | | | 1 | Dicot | Perennial forb | |
| | Apiaceae | SE | 6.0 | 18 | 3 | 6.0 | 0.0 | 0.0 | | 1 | 1 | 1 | | Dicot | Perennial forb | |
| | Apiaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | | | | 1 | Dicot | Perennial forb | |
| | Apiaceae | BE/SI | 3.6 | 21.5 | 6 | 3.5 | 1.9 | 0.8 | | 1 | 1 | 1 | | Dicot | Perennial forb | |
| | <i>Lomatium engelmannii</i> <i>Lomatium hooveri</i> <i>Lomatium howellii</i> <i>Lomatium macrocarpum</i> <i>Lomatium marginatum</i> <i>Lomatium observatorium</i> | Apiaceae | SE | 5.8 | 34.5 | 6 | 6.0 | 0.8 | 0.3 | 4 | 1 | 1 | | | Dicot | Perennial forb |
| | | Apiaceae | SE | 5.9 | 29.5 | 5 | 6.0 | 0.4 | 0.2 | 4 | 1 | | | | Dicot | Perennial forb |
| | | Apiaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 4 | 1 | | | | Dicot | Perennial forb |
| | | Apiaceae | SI | 2.7 | 8 | 3 | 3.0 | 0.6 | 0.3 | | 1 | 1 | 1 | | Dicot | Perennial forb |
| Apiaceae | | BE | 5.0 | 25 | 5 | 6.0 | 1.4 | 0.6 | | 1 | | | 1 | Dicot | Perennial forb | |
| <i>Lomatium parvifolium</i> <i>Lomatium repostum</i> <i>Lomatium tracyi</i> <i>Lomatium triternatum</i> var. <i>triternatum</i> | Apiaceae | WI/IN | 1.4 | 2.75 | 2 | 1.4 | 0.9 | 0.6 | | 1 | 1 | | | Dicot | Perennial forb | |
| | Apiaceae | SI | 3.3 | 13 | 4 | 3.0 | 2.3 | 1.1 | 4 | | | 1 | | Dicot | Perennial forb | |
| | Apiaceae | SI | 3.2 | 12.6 | 4 | 3.0 | 2.4 | 1.2 | 4 | 1 | | | | Dicot | Perennial forb | |
| | Apiaceae | SE | 6.1 | 42.5 | 7 | 6.0 | 0.0 | 0.0 | 4 | 1 | 1 | | | Dicot | Perennial forb | |
| | Apiaceae | SI | 2.8 | 11 | 4 | 2.0 | 2.4 | 1.2 | | 1 | 1 | | | Dicot | Perennial forb | |
| <i>Lomatium utriculatum</i> <i>Perideridia bacigalupii</i> <i>Perideridia kelloggii</i> <i>Perideridia leptocarpa</i> <i>Perideridia oregana</i> <i>Perideridia pringlei</i> <i>Sanicula bipinnatifida</i> <i>Sanicula hoffmannii</i> <i>Sanicula maritima</i> <i>Sanicula peckiana</i> <i>Sanicula tracyi</i> | Apiaceae | WI | 1.7 | 8.5 | 5 | 1.0 | 1.4 | 0.6 | | 1 | 1 | 1 | 1 | Dicot | Perennial forb | |
| | Apiaceae | BE | 4.6 | 23 | 5 | 6.0 | 2.4 | 1.1 | 4 | | | | 1 | Dicot | Perennial forb | |
| | Apiaceae | WI | 2.1 | 10.6 | 5 | 2.0 | 2.0 | 0.9 | | 1 | 1 | 1 | | Dicot | Perennial forb | |
| | Apiaceae | SE | 5.6 | 22.5 | 4 | 6.0 | 1.0 | 0.5 | 4 | 1 | | | | Dicot | Perennial forb | |
| | Apiaceae | WI | 1.7 | 5 | 3 | 1.0 | 1.2 | 0.7 | | 1 | 1 | 1 | | Dicot | Perennial forb | |
| | Apiaceae | BE/SI | 3.7 | 18.5 | 5 | 3.0 | 2.3 | 1.0 | 4 | | | 1 | | Dicot | Perennial forb | |
| | Apiaceae | WI | 1.8 | 7.1 | 4 | 2.0 | 1.5 | 0.7 | | 1 | 1 | 1 | 1 | Dicot | Perennial forb | |
| | Apiaceae | WI | 1.8 | 3.5 | 2 | 1.5 | 2.1 | 1.5 | 4 | | | 1 | | Dicot | Perennial forb | |
| | Apiaceae | WI | 2.3 | 4.5 | 2 | 2.0 | 0.0 | 0.0 | 1b | | | 1 | 1 | Dicot | Perennial forb | |
| | Apiaceae | BE | 5.3 | 26.5 | 5 | 6.0 | 1.3 | 0.6 | 4 | 1 | | | | Dicot | Perennial forb | |
| <i>Sanicula tracyi</i> <i>Sanicula tuberosa</i> <i>Tauschia glauca</i> <i>Tauschia hartwegii</i> <i>Tauschia howellii</i> <i>Tauschia kelloggii</i> | Apiaceae | WI | 2.1 | 8.5 | 4 | 1.0 | 2.6 | 1.3 | | | 1 | | | Dicot | Perennial forb | |
| | Apiaceae | WI/IN | 1.3 | 3.75 | 3 | 1.0 | 0.7 | 0.4 | | 1 | | 1 | 1 | Dicot | Perennial forb | |
| | Apiaceae | BE/SI | 3.5 | 10.5 | 3 | 3.0 | 0.6 | 0.3 | 4 | 1 | | | | Dicot | Perennial forb | |
| | Apiaceae | WI/IN | 1.3 | 4 | 3 | 1.0 | 1.5 | 0.9 | | | 1 | 1 | 1 | Dicot | Perennial forb | |
| | Apiaceae | WI | 2.3 | 7 | 3 | 1.0 | 3.2 | 1.9 | | 1 | | | | Dicot | Perennial forb | |
| Apiaceae | SI | 2.6 | 12.75 | 5 | 2.0 | 2.2 | 1.0 | | | 1 | 1 | 1 | Dicot | Perennial forb | | |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|---|----------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|---|-------|-------------------------|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | | | |
| <i>Asclepias solanoana</i> | Asclepiadaceae | SE | 6.0 | 42 | 7 | 6.0 | 0.0 | 0.0 | 4 | 1 | | | | | | Dicot | Perennial forb | |
| <i>Agoseris heterophylla</i> | Asteraceae | WI/IN | 1.4 | 4.1 | 3 | 1.0 | 1.5 | 0.9 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| <i>Ancistrocarphus flagineus</i> | Asteraceae | SI | 3.3 | 13 | 4 | 3.0 | 0.5 | 0.3 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| <i>Antennaria argentea</i> | Asteraceae | WI | 1.9 | 7.75 | 4 | 0.8 | 2.7 | 1.4 | | 1 | 1 | | | | | Dicot | Perennial forb | |
| <i>Antennaria suffrutescens</i> | Asteraceae | SE | 5.6 | 22.5 | 4 | 6.0 | 1.0 | 0.5 | 4 | 1 | 1 | | | | | Dicot | Perennial forb | |
| <i>Arnica cernua</i> | Asteraceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 4 | 1 | | | | | | Dicot | Perennial forb (rhiz.) | |
| <i>Arnica spathulata</i> | Asteraceae | SE | 5.5 | 16.5 | 3 | 6.0 | 1.2 | 0.7 | 4 | 1 | | | | | | Dicot | Perennial forb (rhiz.) | |
| <i>Aster oregonensis</i> | Asteraceae | WI/IN | 1.1 | 3.25 | 3 | 1.0 | 0.9 | 0.5 | | 1 | 1 | | | 1 | | Dicot | Perennial forb | |
| <i>Balsamorhiza macrolepis</i> var. <i>macrolepis</i> | Asteraceae | SI | 2.5 | 15 | 6 | 2.0 | 1.1 | 0.5 | 1b | | | 1 | | 1 | | Dicot | Perennial forb | |
| <i>Balsamorhiza sericea</i> | Asteraceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | 1 | | | | | | Dicot | Perennial forb | |
| <i>Brickellia greenei</i> | Asteraceae | BE/SI | 3.7 | 11 | 3 | 4.0 | 0.6 | 0.3 | | 1 | 1 | | | 1 | | Dicot | Perennial forb | |
| <i>Cacaliopsis nardosmia</i> | Asteraceae | WI/IN | 1.3 | 4 | 3 | 2.0 | 1.2 | 0.7 | | 1 | | | | 1 | | Dicot | Perennial forb | |
| <i>Calycadenia multiglandulosa</i> | Asteraceae | SI | 3.1 | 15.5 | 5 | 3.0 | 1.2 | 0.6 | | 1 | 1 | 1 | 1 | | | Dicot | Annual forb | |
| <i>Calycadenia oppositifolia</i> | Asteraceae | SI | 2.6 | 18 | 7 | 2.0 | 1.6 | 0.6 | 1b | | | | | 1 | | Dicot | Annual forb | |
| <i>Calycadenia pauciflora</i> | Asteraceae | BE | 5.3 | 21 | 4 | 5.5 | 1.0 | 0.5 | | 1 | | | | | | Dicot | Annual forb | |
| <i>Calycadenia truncata</i> | Asteraceae | WI | 2.1 | 12.5 | 6 | 2.5 | 1.1 | 0.5 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| <i>Chaenactis glabriuscula</i> var. <i>glabriuscula</i> | Asteraceae | WI | 1.7 | 5.1 | 3 | 2.0 | 1.5 | 0.9 | | | | 1 | 1 | 1 | 1 | Dicot | Perennial forb | |
| <i>Chaenactis glabriuscula</i> var. <i>heterocarpha</i> | Asteraceae | SI | 2.5 | 10 | 4 | 2.5 | 0.6 | 0.3 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| <i>Chaenactis suffrutescens</i> | Asteraceae | SE | 6.1 | 30.5 | 5 | 6.0 | 0.0 | 0.0 | 1b | 1 | | | | | | Dicot | Perennial forb | |
| <i>Chrysothamnus nauseosus</i> ssp. <i>consimilis</i> | Asteraceae | WI | 1.8 | 8.85 | 5 | 2.0 | 1.5 | 0.7 | | 1 | 1 | | | 1 | | Dicot | Shrub | |
| <i>Cirsium andrewsii</i> | Asteraceae | WI | 1.7 | 5 | 3 | 2.0 | 0.9 | 0.5 | 1b | | | 1 | | | | Dicot | Perennial forb | |
| <i>Cirsium cymosum</i> | Asteraceae | SI | 3.0 | 12 | 4 | 2.0 | 2.0 | 1.0 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Perennial forb | |
| <i>Cirsium douglasii</i> var. <i>breweri</i> | Asteraceae | SI | 3.0 | 12 | 4 | 3.0 | 1.6 | 0.8 | | 1 | 1 | | | 1 | | Dicot | Perennial forb | |
| <i>Cirsium fontinale</i> var. <i>campylon</i> | Asteraceae | SE | 5.9 | 29.5 | 5 | 6.0 | 0.4 | 0.2 | 1b | | | 1 | 1 | | | Dicot | Perennial forb | |
| <i>Cirsium fontinale</i> var. <i>fontinale</i> | Asteraceae | SE | 6.1 | 30.5 | 5 | 6.0 | 0.0 | 0.0 | 1b | | | 1 | 1 | | | Dicot | Perennial forb | |
| <i>Cirsium fontinale</i> var. <i>obispoense</i> | Asteraceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | | | 1 | | Dicot | Perennial forb | |
| <i>Cirsium hydrophilum</i> var. <i>vaseyi</i> | Asteraceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | 1 | 1 | | | Dicot | Perennial forb | |
| <i>Cirsium remotifolium</i> | Asteraceae | WI/IN | 1.0 | 3.1 | 3 | 1.0 | 1.0 | 0.5 | | 1 | 1 | 1 | | | | Dicot | Perennial forb | |
| <i>Coreopsis stillmanii</i> | Asteraceae | SI | 2.7 | 8 | 3 | 3.0 | 0.6 | 0.3 | | 1 | | 1 | | 1 | | Dicot | Annual forb | |
| <i>Crepis pleurocarpa</i> | Asteraceae | WI | 2.0 | 10 | 5 | 2.0 | 0.7 | 0.3 | | 1 | 1 | | | 1 | | Dicot | Perennial forb | |
| <i>Ericameria arborescens</i> | Asteraceae | WI/IN | 1.3 | 4 | 3 | 1.0 | 1.5 | 0.9 | | 1 | 1 | | | 1 | | Dicot | Shrub | |
| <i>Ericameria greenii</i> | Asteraceae | WI | 2.0 | 8.1 | 4 | 1.5 | 2.1 | 1.1 | | 1 | 1 | | | 1 | 1 | Dicot | Shrub | |
| <i>Ericameria ophitidis</i> | Asteraceae | SE | 5.5 | 38.5 | 7 | 6.0 | 1.0 | 0.4 | 4 | 1 | 1 | | | 1 | | Dicot | Shrub | |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|---|------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|-------|-------------------------|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | | |
| <i>Erigeron angustatus</i> | Asteraceae | SE | 5.7 | 28.5 | 5 | 6.0 | 0.9 | 0.4 | 1b | | 1 | | | | Dicot | Perennial forb | |
| <i>Erigeron bloomeri</i> var. <i>nudatus</i> | Asteraceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 2 | 1 | | | | | Dicot | Perennial forb | |
| <i>Erigeron cervinus</i> | Asteraceae | SI | 3.3 | 10 | 3 | 4.0 | 3.1 | 1.8 | | 1 | | | | | Dicot | Perennial forb (rhiz.) | |
| <i>Erigeron decumbens</i> var. <i>robustior</i> | Asteraceae | WI | 1.5 | 4.5 | 3 | 2.0 | 1.2 | 0.7 | 4 | | 1 | | | | Dicot | Perennial forb | |
| <i>Erigeron foliosus</i> var. <i>confinis</i> | Asteraceae | BE/SI | 3.7 | 11 | 3 | 3.0 | 1.2 | 0.7 | | 1 | | | | | Dicot | Perennial forb | |
| <i>Erigeron lassenianus</i> var. <i>deficiens</i> | Asteraceae | WI | 1.7 | 5 | 3 | 2.0 | 1.5 | 0.9 | | | | | 1 | | Dicot | Perennial forb | |
| <i>Erigeron petrophilus</i> var. <i>sterrensis</i> | Asteraceae | BE | 4.8 | 28.5 | 6 | 6.0 | 2.1 | 0.8 | 4 | | | | 1 | | Dicot | Perennial forb (rhiz.) | |
| <i>Erigeron petrophilus</i> var. <i>viscidulus</i> | Asteraceae | WI | 2.4 | 9.5 | 4 | 2.0 | 0.5 | 0.3 | 4 | 1 | | | | | Dicot | Perennial forb (rhiz.) | |
| <i>Erigeron reductus</i> | Asteraceae | WI | 2.0 | 8 | 4 | 2.0 | 1.6 | 0.8 | | 1 | 1 | | | 1 | Dicot | Perennial forb | |
| <i>Erigeron serpentinus</i> | Asteraceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | | 1 | | | | Dicot | Perennial forb | |
| <i>Eriophyllum conferiflorum</i> var. <i>tanacetiflorum</i> | Asteraceae | WI | 1.9 | 3.75 | 2 | 1.9 | 1.6 | 1.1 | | | | | 1 | | Dicot | Shrub | |
| <i>Eriophyllum jepsonii</i> | Asteraceae | BE/SI | 3.5 | 17.5 | 5 | 3.0 | 1.5 | 0.7 | 4 | | 1 | 1 | | | Dicot | Shrub | |
| <i>Eriophyllum lanatum</i> var. <i>achillaeoides</i> | Asteraceae | WI | 2.3 | 7 | 3 | 2.0 | 0.6 | 0.3 | | 1 | 1 | 1 | 1 | 1 | Dicot | Shrub | |
| <i>Eriophyllum lanatum</i> var. <i>lanceolatum</i> | Asteraceae | WI | 1.7 | 5 | 3 | 2.0 | 1.5 | 0.9 | | 1 | 1 | | | | Dicot | Shrub | |
| <i>Eriophyllum latilobum</i> | Asteraceae | SE | 5.5 | 16.5 | 3 | 6.0 | 1.2 | 0.7 | 1b | | | 1 | 1 | | Dicot | Shrub | |
| <i>Grindelia hirsutula</i> var. <i>davyi</i> | Asteraceae | WI | 1.8 | 5.25 | 3 | 2.0 | 1.4 | 0.8 | | 1 | | | | 1 | Dicot | Perennial forb | |
| <i>Grindelia hirsutula</i> var. <i>hirsutula</i> | Asteraceae | WI/IN | 1.2 | 3.6 | 3 | 1.0 | 1.0 | 0.5 | | | 1 | 1 | | | Dicot | Perennial forb | |
| <i>Grindelia hirsutula</i> var. <i>maritima</i> | Asteraceae | WI | 1.7 | 5 | 3 | 2.0 | 0.9 | 0.5 | 1b | | 1 | | | | Dicot | Perennial forb | |
| <i>Gutierrezia californica</i> | Asteraceae | WI | 1.8 | 5.25 | 3 | 2.0 | 1.4 | 0.8 | | | 1 | 1 | 1 | | Dicot | Perennial forb, Shrub | |
| <i>Harmonia guggolziorum</i> | Asteraceae | SE | 6.0 | 18 | 3 | 6.0 | 0.0 | 0.0 | 1b | | 1 | | | | Dicot | Annual forb | |
| <i>Hazardia stenolepis</i> | Asteraceae | WI | 2.0 | 6.1 | 3 | 3.0 | 1.7 | 1.0 | | | | | 1 | | Dicot | Shrub (stem succulent) | |
| <i>Hazardia whitneyi</i> var. <i>discoidea</i> | Asteraceae | WI | 1.9 | 5.75 | 3 | 2.0 | 1.1 | 0.7 | | 1 | | | | | Dicot | Perennial forb, Shrub | |
| <i>Hazardia whitneyi</i> var. <i>whitneyi</i> | Asteraceae | WI/IN | 1.0 | 2 | 2 | 1.0 | 1.4 | 1.0 | | | | | | 1 | Dicot | Perennial forb, Shrub | |
| <i>Helenium bigelovii</i> | Asteraceae | SI | 2.9 | 11.5 | 4 | 2.5 | 2.3 | 1.2 | | 1 | 1 | | 1 | 1 | Dicot | Perennial forb | |
| <i>Helianthus exilis</i> | Asteraceae | SE | 5.7 | 45.5 | 8 | 6.0 | 1.1 | 0.4 | 4 | 1 | 1 | | 1 | 1 | Dicot | Annual, Perennial forb | |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|--|------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|--|-------|-------------------------|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | | | |
| <i>Hemizonia congesta</i> ssp. <i>calyculata</i> | Asteraceae | WI | 1.5 | 4.5 | 3 | 2.0 | 1.2 | 0.7 | 4 | 1 | | | | | | Dicot | Annual forb | |
| <i>Hemizonia congesta</i> ssp. <i>congesta</i> | Asteraceae | WI/IN | 1.3 | 4 | 3 | 2.0 | 1.2 | 0.7 | | 1 | 1 | 1 | | | | Dicot | Annual forb | |
| <i>Hemizonia congesta</i> ssp. <i>tracyi</i> | Asteraceae | WI | 1.8 | 5.25 | 3 | 2.0 | 0.7 | 0.4 | 4 | 1 | | | | | | Dicot | Annual forb | |
| <i>Hemizonia halliana</i> | Asteraceae | SI | 3.0 | 12 | 4 | 3.0 | 2.4 | 1.2 | | | | | 1 | | | Dicot | Annual forb | |
| <i>Hesperivax sparsiflora</i> var. <i>sparsiflora</i> | Asteraceae | WI | 1.8 | 7.25 | 4 | 1.5 | 1.6 | 0.8 | | 1 | 1 | 1 | 1 | | | Dicot | Annual forb | |
| <i>Heterotheca oregona</i> var. <i>oregona</i> | Asteraceae | WI | 2.0 | 6 | 3 | 3.0 | 1.7 | 1.0 | | 1 | 1 | | 1 | | | Dicot | Perennial forb | |
| <i>Hieracium bolanderi</i> | Asteraceae | BE/SI | 3.8 | 15 | 4 | 4.5 | 2.6 | 1.3 | | 1 | 1 | | | | | Dicot | Perennial forb | |
| <i>Hieracium greenei</i> | Asteraceae | WI | 2.2 | 6.5 | 3 | 3.0 | 1.4 | 0.8 | | 1 | | | | | | Dicot | Perennial forb | |
| <i>Lagophylla glandulosa</i> | Asteraceae | WI | 2.0 | 6.1 | 3 | 3.0 | 1.7 | 1.0 | | 1 | | | | 1 | | Dicot | Annual forb | |
| <i>Lagophylla minor</i> | Asteraceae | BE | 4.7 | 23.5 | 5 | 5.0 | 1.7 | 0.7 | | 1 | | | | 1 | | Dicot | Annual forb | |
| <i>Layia discoidea</i> | Asteraceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | | 1 | | | Dicot | Annual forb | |
| <i>Layia jonesii</i> | Asteraceae | BE/SI | 3.5 | 10.5 | 3 | 3.0 | 0.6 | 0.3 | 1b | | | | 1 | | | Dicot | Annual forb | |
| <i>Layia septentrionalis</i> | Asteraceae | SI | 3.2 | 19 | 6 | 3.5 | 1.4 | 0.6 | 1b | 1 | | | | | | Dicot | Annual forb | |
| <i>Lessingia arachnoidea</i> | Asteraceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | | | 1 | | | | Dicot | Annual forb | |
| <i>Lessingia filaginifolia</i> var. <i>californica</i> | Asteraceae | WI/IN | 1.3 | 4 | 3 | 1.0 | 1.5 | 0.9 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Perennial forb, Shrub | |
| <i>Lessingia hololeuca</i> | Asteraceae | SI | 2.5 | 7.5 | 3 | 3.0 | 1.2 | 0.7 | 3 | 1 | 1 | | | | | Dicot | Annual forb | |
| <i>Lessingia micradenia</i> var. <i>glabrata</i> | Asteraceae | BE | 5.1 | 30.5 | 6 | 5.5 | 1.3 | 0.5 | 1b | | | 1 | | | | Dicot | Annual forb | |
| <i>Lessingia micradenia</i> var. <i>micradenia</i> | Asteraceae | BE | 5.3 | 31.5 | 6 | 5.5 | 1.0 | 0.4 | 1b | | | 1 | | | | Dicot | Annual forb | |
| <i>Lessingia nemaclada</i> | Asteraceae | WI | 2.0 | 6 | 3 | 2.0 | 1.0 | 0.6 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| <i>Lessingia occidentalis</i> | Asteraceae | BE/SI | 4.1 | 16.5 | 4 | 4.0 | 1.8 | 0.9 | 4 | | | | 1 | | | Dicot | Annual forb | |
| <i>Lessingia ramulosa</i> | Asteraceae | BE | 5.4 | 27 | 5 | 6.0 | 1.3 | 0.6 | | 1 | | | | 1 | | Dicot | Annual forb | |
| <i>Luina hypoleuca</i> | Asteraceae | WI/IN | 1.4 | 4.25 | 3 | 2.0 | 1.0 | 0.6 | | 1 | 1 | 1 | | | | Dicot | Perennial forb | |
| <i>Madia doris-nilesiae</i> (= <i>Harmonia d.</i>) | Asteraceae | BE | 5.4 | 32.5 | 6 | 5.5 | 0.8 | 0.3 | 1b | 1 | | | | | | Dicot | Annual forb | |
| <i>Madia exigua</i> | Asteraceae | WI | 1.8 | 7.25 | 4 | 2.0 | 1.4 | 0.7 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| <i>Madia hallii</i> (= <i>Harmonia h.</i>) | Asteraceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | 1 | | | | | | Dicot | Annual forb | |
| <i>Madia stebbinsii</i> (= <i>Harmonia s.</i>) | Asteraceae | SE | 6.1 | 42.5 | 7 | 6.0 | 0.0 | 0.0 | 1b | 1 | | | | | | Dicot | Annual forb | |
| <i>Malacothrix clevelandii</i> | Asteraceae | SI | 3.0 | 9.1 | 3 | 3.0 | 3.0 | 1.7 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| <i>Malacothrix floccifera</i> | Asteraceae | WI | 2.1 | 6.25 | 3 | 3.0 | 1.6 | 0.9 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| <i>Micropus amphibolus</i> | Asteraceae | WI | 2.4 | 7.25 | 3 | 1.0 | 3.1 | 1.8 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| <i>Microseris douglasii</i> | Asteraceae | WI/IN | 1.3 | 4 | 3 | 1.0 | 0.6 | 0.3 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| <i>Monolopia gracilens</i> | Asteraceae | WI | 2.4 | 4.75 | 2 | 2.4 | 2.3 | 1.6 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| <i>Pentachaeta bellidiflora</i> | Asteraceae | WI | 2.4 | 7.25 | 3 | 3.0 | 1.3 | 0.8 | 1b | | | | | 1 | | Dicot | Annual forb | |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|--|---------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|-------|-------------------------|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | |
| <i>Pyrrocoma racemosa</i> var. <i>congesta</i> | Asteraceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 2 | 1 | | | | Dicot | Perennial forb | |
| <i>Pyrrocoma racemosa</i> var. <i>pinetorum</i> | Asteraceae | BE/SI | 4.0 | 16 | 4 | 4.5 | 2.4 | 1.2 | | 1 | | | | Dicot | Perennial forb | |
| <i>Pyrrocoma racemosa</i> var. <i>racemosa</i> | Asteraceae | WI | 1.7 | 5 | 3 | 1.0 | 2.1 | 1.2 | | 1 | 1 | 1 | | Dicot | Perennial forb | |
| <i>Raillardella pringlei</i> | Asteraceae | SE | 6.0 | 30 | 5 | 6.0 | 0.0 | 0.0 | 1b | 1 | | | | Dicot | Perennial forb | |
| <i>Rigipappus leptocladius</i> | Asteraceae | WI | 1.9 | 7.5 | 4 | 2.0 | 1.3 | 0.7 | | 1 | 1 | 1 | 1 | Dicot | Annual forb | |
| <i>Rudbeckia californica</i> var. <i>glauca</i> | Asteraceae | BE | 5.3 | 21 | 4 | 6.0 | 1.5 | 0.8 | | 1 | 1 | | | Dicot | Perennial forb | |
| <i>Senecio clevelandii</i> var. <i>clevelandii</i> (= <i>Packera c. v. c.</i>) | Asteraceae | SE | 5.8 | 46.5 | 8 | 6.0 | 0.7 | 0.3 | 4 | 1 | | | | Dicot | Perennial forb | |
| <i>Senecio clevelandii</i> var. <i>heterophyllus</i> (= <i>Packera c. v. h.</i>) | Asteraceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | | 1 | Dicot | Perennial forb | |
| <i>Senecio eurycephalus</i> var. <i>eurycephalus</i> (= <i>Packera eurycephala</i> var. <i>eurycephala</i>) | Asteraceae | BE/SI | 3.8 | 15 | 4 | 3.0 | 1.5 | 0.8 | | 1 | 1 | | | Dicot | Perennial forb | |
| <i>Senecio eurycephalus</i> var. <i>lewisroei</i> (= <i>Packera eurycephala</i> var. <i>lewisroei</i>) | Asteraceae | SE | 5.8 | 40.5 | 7 | 6.0 | 0.8 | 0.3 | 1b | | | | 1 | Dicot | Perennial forb | |
| <i>Senecio greenei</i> (= <i>Packera g.</i>) | Asteraceae | BE | 5.3 | 32 | 6 | 6.0 | 1.6 | 0.7 | | 1 | 1 | | | Dicot | Perennial forb | |
| <i>Senecio layneae</i> (= <i>Packera l.</i>) | Asteraceae | BE | 4.9 | 29.5 | 6 | 5.0 | 1.3 | 0.5 | 1b | | | | 1 | Dicot | Perennial forb | |
| <i>Senecio macounii</i> (= <i>Packera m.</i>) | Asteraceae | BE | 5.1 | 20.5 | 4 | 6.0 | 2.0 | 1.0 | 4 | 1 | | | | Dicot | Perennial forb | |
| <i>Solidago guiradonis</i> | Asteraceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 4 | | | 1 | | Dicot | Perennial forb | |
| <i>Solidago multiradiata</i> | Asteraceae | WI/IN | 1.1 | 2.1 | 2 | 1.1 | 1.3 | 1.0 | | 1 | | | 1 | Dicot | Perennial forb | |
| <i>Stebbinsoseris decipiens</i> | Asteraceae | WI | 1.8 | 5.5 | 3 | 2.0 | 0.6 | 0.3 | 1b | | 1 | 1 | | Dicot | Annual forb | |
| <i>Wyethia bolanderi</i> | Asteraceae | WI | 1.5 | 3 | 2 | 1.5 | 0.7 | 0.5 | | | | | 1 | Dicot | Perennial forb | |
| <i>Berberis aquifolium</i> var. <i>aquifolium</i> | Berberidaceae | WI | 1.6 | 4.75 | 3 | 1.0 | 1.2 | 0.7 | | 1 | 1 | | 1 | Dicot | Shrub | |
| <i>Berberis aquifolium</i> var. <i>repens</i> | Berberidaceae | WI | 1.7 | 5 | 3 | 1.0 | 1.2 | 0.7 | | 1 | 1 | | 1 | Dicot | Shrub | |
| <i>Vancouveria chrysantha</i> | Berberidaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 4 | 1 | 1 | | | Dicot | Perennial forb (rhiz.) | |
| <i>Vancouveria planipetala</i> | Berberidaceae | WI | 1.7 | 5 | 3 | 1.0 | 1.2 | 0.7 | | 1 | 1 | 1 | 1 | Dicot | Perennial forb (rhiz.) | |
| <i>Cryptantha clevelandii</i> var. <i>dissita</i> | Boraginaceae | BE/SI | 4.4 | 17.5 | 4 | 4.5 | 2.1 | 1.0 | 1b | | 1 | | | Dicot | Annual forb | |
| <i>Cryptantha excavata</i> | Boraginaceae | WI | 1.5 | 3 | 2 | 1.5 | 2.1 | 1.5 | | 1 | | | | Dicot | Annual forb | |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | | Tax. ¹⁰ | |
|--|--------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|--------------------|------------------------|--------------------|--|
| | | | | | | | | | | KL | NC | BA | SC | SN | Cat. ¹⁰ | Lifeform ¹¹ | | |
| <i>Cryptantha flaccida</i> | Boraginaceae | WI | 1.6 | 4.75 | 3 | 2.0 | 0.7 | 0.4 | | 1 | 1 | 1 | 1 | 1 | Dicot | Annual forb | | |
| <i>Cryptantha hispida</i> | Boraginaceae | SE | 6.0 | 24 | 4 | 6.0 | 0.0 | 0.0 | | 1 | 1 | | | | Dicot | Annual forb | | |
| <i>Cryptantha intermedia</i> | Boraginaceae | WI/IN | 1.4 | 4.1 | 3 | 1.0 | 1.5 | 0.9 | | 1 | 1 | 1 | 1 | 1 | Dicot | Annual forb | | |
| <i>Cryptantha mariposae</i> | Boraginaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | | | | | | Dicot | Annual forb | | |
| <i>Cryptantha milobakeri</i> | Boraginaceae | SI | 3.3 | 9.75 | 3 | 3.0 | 2.6 | 1.5 | | 1 | 1 | 1 | 1 | 1 | Dicot | Annual forb | | |
| <i>Cryptantha sobolifera</i> | Boraginaceae | WI/IN | 1.4 | 4.1 | 3 | 1.0 | 1.5 | 0.9 | | 1 | | | | | Dicot | Perennial forb | | |
| <i>Hackelia bella</i> | Boraginaceae | WI/IN | 1.3 | 4 | 3 | 1.0 | 1.5 | 0.9 | | 1 | 1 | | | | Dicot | Perennial forb | | |
| <i>Pectocarya pusilla</i> | Boraginaceae | WI/IN | 1.3 | 2.5 | 2 | 1.3 | 1.1 | 0.8 | | 1 | 1 | 1 | 1 | 1 | Dicot | Annual forb | | |
| <i>Arabis aculeolata</i> | Brassicaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 2 | 1 | | | | | Dicot | Perennial forb | | |
| <i>Arabis constancei</i> | Brassicaceae | SE | 5.9 | 41.5 | 7 | 6.0 | 0.4 | 0.1 | 1b | | | | | 1 | Dicot | Perennial forb | | |
| <i>Arabis koehleri</i> var. <i>stipitata</i> | Brassicaceae | SE | 5.5 | 16.5 | 3 | 6.0 | 1.2 | 0.7 | 1b | 1 | | | | | Dicot | Perennial forb | | |
| <i>Arabis macdonaldiana</i> | Brassicaceae | BE | 5.4 | 32.5 | 6 | 6.0 | 1.0 | 0.4 | 1b | 1 | 1 | | | | Dicot | Perennial forb | | |
| <i>Arabis oregana</i> | Brassicaceae | BE/SI | 3.8 | 11.5 | 3 | 3.0 | 2.1 | 1.2 | 4 | 1 | 1 | | | | Dicot | Perennial forb | | |
| <i>Arabis subpinnatifida</i> | Brassicaceae | SI | 3.2 | 16 | 5 | 3.0 | 1.6 | 0.7 | | 1 | 1 | | | | Dicot | Perennial forb | | |
| <i>Arabis suffrutescens</i> var. <i>horizontalis</i> | Brassicaceae | BE/SI | 3.9 | 27 | 7 | 3.0 | 1.6 | 0.6 | | | 1 | | | 1 | Dicot | Perennial forb | | |
| <i>Arabis suffrutescens</i> var. <i>suffrutescens</i> | Brassicaceae | SI | 2.9 | 17.5 | 6 | 2.5 | 1.9 | 0.8 | | 1 | | | | 1 | Dicot | Perennial forb | | |
| <i>Cardamine californica</i> var. <i>cuneata</i> | Brassicaceae | WI | 1.9 | 3.75 | 2 | 1.9 | 1.6 | 1.1 | | | | 1 | | | Dicot | Perennial forb (rhiz.) | | |
| <i>Cardamine nuttallii</i> var. <i>gemmata</i> | Brassicaceae | BE | 5.2 | 15.5 | 3 | 5.0 | 1.0 | 0.6 | 1b | 1 | | | | | Dicot | Perennial forb (rhiz.) | | |
| <i>Cardamine pachystigma</i> var. <i>dissectifolia</i> | Brassicaceae | BE | 5.4 | 48.5 | 9 | 6.0 | 1.0 | 0.3 | 3 | | 1 | | | 1 | Dicot | Perennial forb (rhiz.) | | |
| <i>Cardamine pachystigma</i> var. <i>pachystigma</i> | Brassicaceae | WI | 2.0 | 6 | 3 | 2.0 | 1.0 | 0.6 | | 1 | | | | 1 | Dicot | Perennial forb (rhiz.) | | |
| <i>Caulanthus amplexicaulis</i> var. <i>barbarea</i> | Brassicaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | | | | 1 | | Dicot | Annual forb | | |
| <i>Draba aureola</i> | Brassicaceae | SI | 2.7 | 8 | 3 | 3.0 | 0.6 | 0.3 | 1b | 1 | | | | | Dicot | Perennial forb | | |
| <i>Draba carnosula</i> | Brassicaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | 1 | | | | | Dicot | Perennial forb | | |
| <i>Draba howellii</i> | Brassicaceae | WI/IN | 1.4 | 4.25 | 3 | 1.0 | 1.4 | 0.8 | | 1 | | | | | Dicot | Perennial forb | | |
| <i>Erysimum franciscanum</i> | Brassicaceae | SI | 3.0 | 9 | 3 | 3.0 | 0.0 | 0.0 | 4 | | 1 | 1 | 1 | | Dicot | Perennial forb | | |
| <i>Guillenia flavescens</i> | Brassicaceae | WI | 2.3 | 9.25 | 4 | 2.5 | 1.6 | 0.8 | | 1 | 1 | 1 | 1 | | Dicot | Annual forb | | |
| <i>Streptanthus albidus</i> ssp. <i>albidus</i> | Brassicaceae | BE | 5.3 | 31.5 | 6 | 6.0 | 1.3 | 0.5 | 1b | | 1 | 1 | 1 | | Dicot | Annual forb | | |
| <i>Streptanthus albidus</i> ssp. <i>peramoenus</i> | Brassicaceae | BE/SI | 4.3 | 34.5 | 8 | 4.5 | 1.9 | 0.7 | 1b | | | 1 | 1 | | Dicot | Annual forb | | |
| <i>Streptanthus barbatus</i> | Brassicaceae | SE | 5.6 | 28 | 5 | 6.0 | 0.5 | 0.2 | | 1 | | | | | Dicot | Perennial forb | | |
| <i>Streptanthus barbiger</i> | Brassicaceae | SE | 6.0 | 24 | 4 | 6.0 | 0.0 | 0.0 | 4 | | 1 | | | | Dicot | Annual forb | | |
| <i>Streptanthus batrachopus</i> | Brassicaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | 1 | 1 | | 1 | Dicot | Annual forb | | |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|--|--------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|--|-------------------------|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | | |
| <i>Streptanthus brachiatus</i> var. <i>brachiatus</i> | Brassicaceae | SE | 5.6 | 22.5 | 4 | 6.0 | 1.0 | 0.5 | 1b | | 1 | | | | | Dicot | Annual, Perennial forb |
| <i>Streptanthus brachiatus</i> var. <i>hoffmanii</i> | Brassicaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | 1 | | | | | Dicot | Annual, Perennial forb |
| <i>Streptanthus breweri</i> var. <i>breweri</i> | Brassicaceae | SE | 5.7 | 40 | 7 | 6.0 | 0.8 | 0.3 | | 1 | 1 | 1 | 1 | | | Dicot | Annual forb |
| <i>Streptanthus breweri</i> var. <i>hesperidus</i> | Brassicaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | 1 | | | | | Dicot | Annual forb |
| <i>Streptanthus drepanoides</i> | Brassicaceae | SE | 6.1 | 36.5 | 6 | 6.0 | 0.0 | 0.0 | 4 | 1 | 1 | | | 1 | | Dicot | Annual forb |
| <i>Streptanthus glandulosus</i> ssp. <i>glandulosus</i> | Brassicaceae | WI | 1.9 | 5.75 | 3 | 2.0 | 1.1 | 0.7 | | 1 | 1 | 1 | 1 | | | Dicot | Annual forb |
| <i>Streptanthus glandulosus</i> ssp. <i>pulchellus</i> | Brassicaceae | BE | 4.9 | 24.5 | 5 | 6.0 | 1.8 | 0.8 | 1b | | 1 | 1 | | | | Dicot | Annual forb |
| <i>Streptanthus glandulosus</i> ssp. <i>secundus</i> | Brassicaceae | SI | 3.3 | 20 | 6 | 3.0 | 1.5 | 0.6 | | 1 | 1 | | | | | Dicot | Annual forb |
| <i>Streptanthus glandulosus</i> ssp. <i>secundus</i> var. <i>hoffmanii</i> | Brassicaceae | SI | 3.0 | 3 | 1 | 3.0 | — | — | 1b | | 1 | | | | | Dicot | Annual forb |
| <i>Streptanthus howellii</i> | Brassicaceae | SE | 6.1 | 30.5 | 5 | 6.0 | 0.0 | 0.0 | 1b | 1 | | | | | | Dicot | Perennial forb |
| <i>Streptanthus insignis</i> ssp. <i>insignis</i> | Brassicaceae | BE/SI | 4.0 | 20 | 5 | 4.0 | 2.4 | 1.1 | | | | | 1 | | | Dicot | Annual forb |
| <i>Streptanthus insignis</i> ssp. <i>lyonii</i> | Brassicaceae | SI | 3.3 | 16.5 | 5 | 2.0 | 2.7 | 1.2 | 1b | | | | 1 | | | Dicot | Annual forb |
| <i>Streptanthus morrissonii</i> ssp. <i>elatus</i> | Brassicaceae | SE | 6.1 | 30.5 | 5 | 6.0 | 0.0 | 0.0 | 1b | | 1 | | | | | Dicot | Annual, Perennial forb |
| <i>Streptanthus morrissonii</i> ssp. <i>hirtiflorus</i> | Brassicaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | 1 | | | | | Dicot | Annual, Perennial forb |
| <i>Streptanthus morrissonii</i> ssp. <i>kruckebergii</i> | Brassicaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | 1 | | | | | Dicot | Annual, Perennial forb |
| <i>Streptanthus morrissonii</i> ssp. <i>morrissonii</i> | Brassicaceae | SE | 6.1 | 30.5 | 5 | 6.0 | 0.0 | 0.0 | 1b | | 1 | | | | | Dicot | Annual, Perennial forb |
| <i>Streptanthus niger</i> | Brassicaceae | SE | 6.1 | 30.5 | 5 | 6.0 | 0.0 | 0.0 | 1b | | 1 | 1 | | | | Dicot | Annual forb |
| <i>Streptanthus polygaloides</i> | Brassicaceae | SE | 5.7 | 28.5 | 5 | 6.0 | 0.9 | 0.4 | | | | | | 1 | | Dicot | Annual forb |
| <i>Streptanthus tortuosus</i> var. <i>suffrutescens</i> | Brassicaceae | WI | 1.6 | 8.2 | 5 | 2.0 | 1.6 | 0.7 | | 1 | | 1 | 1 | 1 | | Dicot | Annual, Perennial forb |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|---|-----------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|-------|--|-------------------------|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | | |
| <i>Streptanthus tortuosus</i> var. <i>tortuosus</i> | Brassicaceae | WI/IN | 1.4 | 4.25 | 3 | 2.0 | 1.0 | 0.6 | | 1 | 1 | | 1 | Dicot | | Annual, Perennial forb | |
| <i>Thelypodium brachycarpum</i> | Brassicaceae | SI | 3.3 | 10 | 3 | 3.0 | 0.6 | 0.3 | 4 | 1 | | | | Dicot | | Annual, Perennial forb | |
| <i>Thlaspi californicum</i> | Brassicaceae | SE | 6.1 | 30.5 | 5 | 6.0 | 0.0 | 0.0 | 1b | | | | | Dicot | | Perennial forb | |
| <i>Thlaspi montanum</i> var. <i>montanum</i> | Brassicaceae | BE/SI | 4.4 | 22 | 5 | 4.0 | 1.5 | 0.7 | | 1 | 1 | | | Dicot | | Perennial forb | |
| <i>Campanula angustiflora</i> | Campanulaceae | BE/SI | 3.9 | 19.25 | 5 | 4.0 | 2.4 | 1.1 | | 1 | 1 | | | Dicot | | Annual forb | |
| <i>Campanula exigua</i> | Campanulaceae | BE/SI | 3.9 | 19.5 | 5 | 4.0 | 1.5 | 0.7 | 1b | | | 1 | 1 | Dicot | | Annual forb | |
| <i>Campanula griffinii</i> | Campanulaceae | SE | 6.0 | 18 | 3 | 6.0 | 0.0 | 0.0 | | | 1 | 1 | 1 | Dicot | | Annual forb | |
| <i>Campanula rotundifolia</i> | Campanulaceae | BE | 5.0 | 15 | 3 | 6.0 | 1.7 | 1.0 | | | 1 | | | Dicot | | Perennial forb | |
| <i>Campanula scabrella</i> | Campanulaceae | SI | 2.5 | 10 | 4 | 2.5 | 1.3 | 0.6 | 4 | 1 | | | | Dicot | | Perennial forb (rhiz.) | |
| <i>Campanula sharsmithiae</i> | Campanulaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | | 1 | 1 | | Dicot | | Annual forb | |
| <i>Campanula wilkinsiana</i> | Campanulaceae | WI/IN | 1.0 | 5 | 5 | 0.0 | 1.7 | 0.8 | | 1 | | | | Dicot | | Perennial forb (rhiz.) | |
| <i>Githopsis diffusa</i> ssp. <i>candida</i> | Campanulaceae | WI/IN | 1.0 | 2 | 2 | 1.0 | 1.4 | 1.0 | | | 1 | | | Dicot | | Annual forb | |
| <i>Githopsis pulchella</i> ssp. <i>campestris</i> | Campanulaceae | WI | 1.6 | 3.25 | 2 | 1.6 | 1.9 | 1.4 | | | | | 1 | Dicot | | Annual forb | |
| <i>Githopsis pulchella</i> ssp. <i>pulchella</i> var. <i>glabra</i> | Campanulaceae | BE/SI | 3.8 | 19 | 5 | 3.0 | 2.0 | 0.9 | | | | | 1 | Dicot | | Annual forb | |
| <i>Githopsis pulchella</i> ssp. <i>serpentinicola</i> | Campanulaceae | BE | 5.3 | 21 | 4 | 5.5 | 1.0 | 0.5 | 4 | | | | 1 | Dicot | | Annual forb | |
| <i>Nemacladus montanus</i> | Campanulaceae | SE | 6.0 | 18 | 3 | 6.0 | 0.0 | 0.0 | | 1 | 1 | 1 | | Dicot | | Annual forb | |
| <i>Arenaria kingii</i> var. <i>glabrescens</i> | Caryophyllaceae | WI/IN | 1.4 | 4.1 | 3 | 2.0 | 1.1 | 0.6 | | | | | 1 | Dicot | | Perennial forb | |
| <i>Cerastium arvense</i> | Caryophyllaceae | WI | 2.1 | 8.5 | 4 | 0.9 | 2.6 | 1.3 | | 1 | 1 | 1 | 1 | Dicot | | Perennial forb | |
| <i>Minuartia californica</i> | Caryophyllaceae | WI | 1.7 | 5 | 3 | 2.0 | 1.5 | 0.9 | | 1 | 1 | 1 | 1 | Dicot | | Annual forb | |
| <i>Minuartia cismontana</i> (new taxon) | Caryophyllaceae | WI | 1.8 | 3.5 | 2 | 1.8 | 1.8 | 1.3 | | 1 | 1 | 1 | 1 | Dicot | | Annual, Perennial forb | |
| <i>Minuartia decumbens</i> | Caryophyllaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | 1 | 1 | | | Dicot | | Perennial forb | |
| <i>Minuartia douglasii</i> | Caryophyllaceae | SI | 3.0 | 15 | 5 | 3.0 | 0.7 | 0.3 | | 1 | 1 | 1 | 1 | Dicot | | Annual forb | |
| <i>Minuartia howellii</i> | Caryophyllaceae | SE | 5.7 | 28.5 | 5 | 6.0 | 0.9 | 0.4 | 1b | 1 | | | | Dicot | | Perennial forb | |
| <i>Minuartia nuttallii</i> ssp. <i>gregaria</i> | Caryophyllaceae | SI | 3.2 | 16 | 5 | 3.0 | 1.9 | 0.9 | | 1 | 1 | | | Dicot | | Perennial forb | |
| <i>Minuartia rosei</i> | Caryophyllaceae | SE | 6.1 | 30.5 | 5 | 6.0 | 0.0 | 0.0 | 4 | 1 | 1 | | | Dicot | | Perennial forb | |
| <i>Minuartia stolonifera</i> | Caryophyllaceae | SE | 6.1 | 30.5 | 5 | 6.0 | 0.0 | 0.0 | 1b | 1 | | | | Dicot | | Perennial forb | |
| <i>Moehringia macrophylla</i> | Caryophyllaceae | SI | 2.7 | 8 | 3 | 3.0 | 0.6 | 0.3 | | 1 | 1 | 1 | 1 | Dicot | | Perennial forb | |
| <i>Silene antirrhina</i> | Caryophyllaceae | WI/IN | 1.1 | 3.25 | 3 | 1.0 | 0.9 | 0.5 | | 1 | 1 | 1 | 1 | Dicot | | Annual forb | |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|--|-----------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|--|----------|-------------------------|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | | | |
| <i>Silene campanulata</i> ssp. <i>campanulata</i> | Caryophyllaceae | BE | 5.3 | 31.5 | 6 | 5.5 | 1.0 | 0.4 | 4 | 1 | 1 | | | | | Dicot | Perennial forb | |
| <i>Silene campanulata</i> ssp. <i>glandulosa</i> | Caryophyllaceae | BE/SI | 3.8 | 19 | 5 | 3.0 | 1.3 | 0.6 | | 1 | 1 | | | | | Dicot | Perennial forb | |
| <i>Silene grayi</i> | Caryophyllaceae | WI | 1.8 | 5.5 | 3 | 2.0 | 1.3 | 0.7 | | 1 | | | | | | Dicot | Perennial forb | |
| <i>Silene hookeri</i> ssp. <i>bolanderi</i> | Caryophyllaceae | BE | 4.5 | 18 | 4 | 4.5 | 1.7 | 0.9 | | 1 | 1 | | | | | Dicot | Perennial forb | |
| <i>Silene hookeri</i> ssp. <i>hookeri</i> | Caryophyllaceae | SI | 3.0 | 12 | 4 | 2.5 | 2.2 | 1.1 | | 1 | 1 | | | | | Dicot | Perennial forb | |
| <i>Silene serpentinicola</i> (new taxon) | Caryophyllaceae | SE | 6.0 | 6 | 1 | 6.0 | — | — | | 1 | | | | | | Dicot | Perennial forb (rhiz.) | |
| <i>Helianthemum suffrutescens</i> (in <i>H. scoparium</i> in Jepson) | Cistaceae | WI/IN | 1.0 | 2 | 2 | 1.0 | 1.4 | 1.0 | 3 | | | | | 1 | | Dicot | Shrub | |
| <i>Calystegia collina</i> ssp. <i>collina</i> | Convolvulaceae | BE | 4.7 | 33 | 7 | 6.0 | 1.6 | 0.6 | | | 1 | 1 | | | | Dicot | Perennial forb | |
| <i>Calystegia collina</i> ssp. <i>oxyphylla</i> | Convolvulaceae | SE | 5.6 | 33.5 | 6 | 6.0 | 1.2 | 0.5 | 4 | | 1 | | | | | Dicot | Perennial forb | |
| <i>Calystegia collina</i> ssp. <i>tridactylosa</i> | Convolvulaceae | BE | 4.5 | 18 | 4 | 4.5 | 1.7 | 0.9 | | 1 | | | | | | Dicot | Perennial forb | |
| <i>Calystegia collina</i> ssp. <i>venusta</i> | Convolvulaceae | BE | 4.9 | 24.5 | 5 | 5.0 | 1.3 | 0.6 | 4 | | | | 1 | | | Dicot | Perennial forb | |
| <i>Calystegia malacophylla</i> | Convolvulaceae | WI | 1.5 | 4.5 | 3 | 1.0 | 1.3 | 0.8 | | | | 1 | 1 | 1 | | Dicot | Perennial forb | |
| <i>Convolvulus simulans</i> | Convolvulaceae | BE/SI | 3.7 | 14.75 | 4 | 4.0 | 2.4 | 1.2 | 4 | | | 1 | | | | Dicot | Annual forb | |
| <i>Dudleya abramsii</i> ssp. <i>betinae</i> | Crassulaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | | | | 1 | | | Dicot | Perennial forb | |
| <i>Dudleya abramsii</i> ssp. <i>murina</i> | Crassulaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | | | | 1 | | | Dicot | Perennial forb | |
| <i>Dudleya blochmaniae</i> ssp. <i>blochmaniae</i> | Crassulaceae | SI | 3.2 | 9.5 | 3 | 3.0 | 0.0 | 0.0 | 1b | | | | 1 | | | Dicot | Perennial forb | |
| <i>Dudleya setchellii</i> | Crassulaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | 1 | 1 | | | Dicot | Perennial forb | |
| <i>Parvisedum pentandrum</i> | Crassulaceae | WI | 2.0 | 8.1 | 4 | 1.5 | 2.1 | 1.1 | | | 1 | 1 | 1 | | | Dicot | Annual forb | |
| <i>Parvisedum pumilum</i> | Crassulaceae | WI | 1.7 | 5.1 | 3 | 2.0 | 1.5 | 0.9 | | | 1 | | | 1 | | Dicot | Annual forb | |
| <i>Sedum albotmarginatum</i> | Crassulaceae | SE | 6.1 | 42.5 | 7 | 6.0 | 0.0 | 0.0 | 1b | | | | | 1 | | Dicot | Perennial forb | |
| <i>Sedum eastwoodiae</i> | Crassulaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | 1 | | | | Dicot | Perennial forb | |
| <i>Sedum laxum</i> ssp. <i>flavidum</i> | Crassulaceae | SI | 3.1 | 18.5 | 6 | 3.0 | 0.6 | 0.3 | 4 | | | 1 | 1 | | | Dicot | Perennial forb | |
| <i>Sedum laxum</i> ssp. <i>heckneri</i> | Crassulaceae | BE/SI | 3.5 | 10.5 | 3 | 3.0 | 0.6 | 0.3 | 4 | | | 1 | 1 | | | Dicot | Perennial forb | |
| <i>Sedum laxum</i> ssp. <i>laxum</i> | Crassulaceae | BE/SI | 4.0 | 16 | 4 | 3.5 | 1.4 | 0.7 | | | 1 | 1 | | | | Dicot | Perennial forb | |
| <i>Sedum obtusatum</i> ssp. <i>obtusatum</i> | Crassulaceae | SI | 3.2 | 16 | 5 | 3.0 | 2.2 | 1.0 | | | 1 | | | 1 | | Dicot | Perennial forb (rhiz.) | |
| <i>Sedum radiatum</i> | Crassulaceae | WI | 2.0 | 6 | 3 | 2.0 | 2.0 | 1.2 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| <i>Calocedrus decurrens</i> | Cupressaceae | SI | 3.0 | 9 | 3 | 3.0 | 0.0 | 0.0 | | 1 | 1 | 1 | 1 | 1 | | Gymnosp. | Tree | |
| <i>Cupressus bakeri</i> | Cupressaceae | SI | 2.6 | 13 | 5 | 3.0 | 0.5 | 0.2 | 4 | | | | | 1 | | Gymnosp. | Tree | |
| <i>Cupressus lawsoniana</i> | Cupressaceae | SI | 3.0 | 15 | 5 | 3.0 | 0.7 | 0.3 | | 1 | 1 | | | | | Gymnosp. | Tree | |
| <i>Cupressus macnabiana</i> | Cupressaceae | BE | 4.7 | 28 | 6 | 4.5 | 1.2 | 0.5 | | | | | | 1 | | Gymnosp. | Tree | |
| <i>Cupressus sargentii</i> | Cupressaceae | BE | 4.9 | 34 | 7 | 5.0 | 1.2 | 0.5 | | | 1 | 1 | 1 | | | Gymnosp. | Tree | |
| <i>Juniperus communis</i> var. <i>jackii</i> | Cupressaceae | BE/SI | 4.0 | 8 | 2 | 4.0 | 2.8 | 2.0 | | 1 | | | | | | Gymnosp. | Shrub | |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|--|-----------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|-------------------------|-------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | |
| <i>Carex amplexans</i> | Cyperaceae | SI | 2.6 | 10.5 | 4 | 2.3 | 2.9 | 1.4 | | | | | 1 | | Monocot | Perennial gram. (cesp.) |
| <i>Carex brainerdii</i> | Cyperaceae | WI/IN | 1.4 | 4.25 | 3 | 2.0 | 1.0 | 0.6 | | 1 | 1 | | 1 | 1 | Monocot | Perennial gram. (rhiz.) |
| <i>Carex gigas</i> | Cyperaceae | BE | 4.5 | 22.5 | 5 | 4.0 | 1.7 | 0.7 | 4 | 1 | | | | 1 | Monocot | Perennial gram. (rhiz.) |
| <i>Carex mendocinensis</i> | Cyperaceae | BE/SI | 3.8 | 23 | 6 | 3.5 | 1.2 | 0.5 | | 1 | 1 | | | 1 | Monocot | Perennial gram. (rhiz.) |
| <i>Carex obispoensis</i> | Cyperaceae | BE | 4.9 | 24.5 | 5 | 6.0 | 1.6 | 0.7 | 1b | | | 1 | | | Monocot | Perennial gram. (cesp.) |
| <i>Carex serpentinicola</i> (new taxon) | Cyperaceae | SE | 5.5 | 11 | 2 | 5.5 | 0.7 | 0.5 | 2 | 1 | | | | | Monocot | Perennial gram. (rhiz.) |
| <i>Carex serratodens</i> | Cyperaceae | BE | 4.9 | 39 | 8 | 5.0 | 1.1 | 0.4 | | 1 | 1 | 1 | | 1 | Monocot | Perennial gram. (cesp.) |
| <i>Carex spissa</i> | Cyperaceae | SI | 2.8 | 8.25 | 3 | 2.0 | 2.9 | 1.7 | | | | 1 | | | Monocot | Perennial gram. (rhiz.) |
| <i>Polystichum lemmonii</i> | Dryopteridaceae | SE | 6.0 | 24 | 4 | 6.0 | 0.0 | 0.0 | | 1 | 1 | | | 1 | Pteridoph. | Perennial forb (rhiz.) |
| <i>Polystichum scopulinum</i> | Dryopteridaceae | WI | 1.7 | 5.1 | 3 | 2.0 | 1.5 | 0.9 | | 1 | 1 | | | 1 | Pteridoph. | Perennial forb (rhiz.) |
| <i>Arctostaphylos bakeri</i> ssp. <i>bakeri</i> | Ericaceae | SE | 5.5 | 27.5 | 5 | 6.0 | 1.3 | 0.6 | 1b | | 1 | | | | Dicot | Shrub |
| <i>Arctostaphylos bakeri</i> ssp. <i>sublaevis</i> | Ericaceae | SE | 6.3 | 12.5 | 2 | 6.0 | 0.0 | 0.0 | 1b | | 1 | | | | Dicot | Shrub |
| <i>Arctostaphylos canescens</i> ssp. <i>sonomensis</i> | Ericaceae | SI | 2.5 | 12.5 | 5 | 3.0 | 1.5 | 0.7 | 1b | 1 | 1 | | | | Dicot | Shrub |
| <i>Arctostaphylos hispidula</i> | Ericaceae | BE | 4.5 | 22.5 | 5 | 4.0 | 1.1 | 0.5 | 4 | 1 | 1 | | | | Dicot | Shrub |
| <i>Arctostaphylos hookeri</i> ssp. <i>franciscana</i> | Ericaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1a | | | 1 | 1 | | Dicot | Shrub |
| <i>Arctostaphylos hookeri</i> ssp. <i>montana</i> | Ericaceae | BE | 4.9 | 19.5 | 4 | 4.5 | 1.0 | 0.5 | 1b | | | 1 | 1 | | Dicot | Shrub |
| <i>Arctostaphylos hookeri</i> ssp. <i>ravenii</i> | Ericaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | | | 1 | 1 | | Dicot | Shrub |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Geog. Dist. ⁹ | | | | | | Tax. Cat. ¹⁰ | | Lifeform ¹¹ |
|---|-----------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|--------------------------|----|----|----|----|----|-------------------------|-------|------------------------|
| | | | | | | | | | Rarity ⁸ | KL | NC | BA | SC | SN | | | |
| <i>Arctostaphylos klamathensis</i> | Ericaceae | BE/SI | 3.9 | 19.5 | 5 | 4.0 | 1.8 | 0.8 | 1b | 1 | | | | | | Dicot | Shrub |
| <i>Arctostaphylos nortensis</i> | Ericaceae | SI | 2.8 | 5.5 | 2 | 2.5 | 0.7 | 0.5 | 4 | 1 | | | | | | Dicot | Shrub |
| <i>Arctostaphylos obispoensis</i> | Ericaceae | SE | 5.7 | 28.5 | 5 | 6.0 | 0.9 | 0.4 | 4 | | | | 1 | | | Dicot | Shrub |
| <i>Arctostaphylos stanfordiana</i> | Ericaceae | SI | 2.6 | 10.5 | 4 | 3.0 | 1.7 | 0.9 | 1b | 1 | | | | | | Dicot | Shrub |
| <i>ssp. raichei</i> | | | | | | | | | | | | | | | | | |
| <i>Arctostaphylos viscida</i> ssp. | Ericaceae | BE | 5.0 | 25 | 5 | 5.0 | 1.0 | 0.4 | | 1 | 1 | | | | | Dicot | Shrub |
| <i>pulchella</i> | | | | | | | | | | | | | | | | | |
| <i>Arctostaphylos viscida</i> ssp. | Ericaceae | WI | 2.2 | 10.75 | 5 | 3.0 | 1.2 | 0.5 | | 1 | | | | 1 | | Dicot | Shrub |
| <i>viscida</i> | | | | | | | | | | | | | | | | | |
| <i>Pyrola picta</i> ssp. <i>dentata</i> | Ericaceae | WI | 2.0 | 6 | 3 | 3.0 | 1.7 | 1.0 | | 1 | 1 | | | | | Dicot | Perennial forb (rhiz.) |
| <i>Vaccinium coccineum</i> | Ericaceae | BE/SI | 3.5 | 3.5 | 1 | 3.0 | — | — | 3 | 1 | | | | | | Dicot | Shrub |
| <i>Astragalus breweri</i> | Fabaceae | SI | 3.2 | 15.75 | 5 | 3.0 | 2.0 | 0.9 | 4 | 1 | 1 | | | | | Dicot | Annual forb |
| <i>Astragalus clarianus</i> (<i>claranus</i>) | Fabaceae | SI | 3.0 | 6 | 2 | 3.0 | 0.0 | 0.0 | 1b | 1 | | | | | | Dicot | Annual forb |
| <i>Astragalus clevelandii</i> | Fabaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 4 | 1 | | | | 1 | | Dicot | Perennial forb |
| <i>Astragalus curtipes</i> | Fabaceae | WI | 1.8 | 3.5 | 2 | 1.8 | 1.8 | 1.3 | | 1 | | | | 1 | | Dicot | Perennial forb |
| <i>Astragalus macradon</i> | Fabaceae | WI/IN | 1.3 | 3.75 | 3 | 1.0 | 0.7 | 0.4 | 4 | | | | | 1 | | Dicot | Perennial forb |
| <i>Astragalus rattanii</i> var. | Fabaceae | BE/SI | 4.3 | 25.5 | 6 | 4.0 | 1.2 | 0.5 | 1b | 1 | | | | | | Dicot | Annual forb |
| <i>jepsonianus</i> | | | | | | | | | | | | | | | | | |
| <i>Astragalus whineyi</i> var. | Fabaceae | BE | 4.6 | 23 | 5 | 5.0 | 1.1 | 0.5 | | 1 | 1 | | | | | Dicot | Perennial forb |
| <i>siskiyouensis</i> | | | | | | | | | | | | | | | | | |
| <i>Hoita strobilina</i> | Fabaceae | SI | 2.5 | 5 | 2 | 2.5 | 2.1 | 1.5 | 1b | | | 1 | | | | Dicot | Perennial forb |
| <i>Lathyrus biflorus</i> | Fabaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | 1 | | | | Dicot | Perennial forb |
| <i>Lathyrus delnoriticus</i> | Fabaceae | BE | 5.3 | 10.5 | 2 | 5.0 | 1.4 | 1.0 | 4 | 1 | | | | | | Dicot | Perennial forb |
| <i>Lathyrus vestitus</i> var. <i>vestitus</i> | Fabaceae | WI | 1.8 | 7.2 | 4 | 0.6 | 2.8 | 1.4 | | 1 | 1 | 1 | | | | Dicot | Perennial forb |
| <i>Lotus junceus</i> var. <i>junceus</i> | Fabaceae | WI | 1.5 | 3 | 2 | 1.5 | 0.7 | 0.5 | | | | | 1 | | | Dicot | Perennial forb |
| <i>Lupinus constancei</i> | Fabaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | | 1 | | | Dicot | Perennial forb |
| <i>Lupinus lapidicola</i> | Fabaceae | SI | 3.0 | 15 | 5 | 3.0 | 3.0 | 1.3 | 4 | 1 | 1 | | | | | Dicot | Perennial forb |
| <i>Lupinus onustus</i> | Fabaceae | SI | 3.1 | 15.25 | 5 | 3.0 | 2.9 | 1.3 | | 1 | | | | | | Dicot | Perennial forb |
| <i>Lupinus spectabilis</i> | Fabaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | | | 1 | | Dicot | Perennial forb |
| <i>Pediometum californicum</i> | Fabaceae | BE/SI | 4.4 | 21.75 | 5 | 6.0 | 2.4 | 1.1 | | 1 | 1 | 1 | | | | Dicot | Annual forb |
| <i>Trifolium amoenum</i> | Fabaceae | WI/IN | 1.3 | 2.5 | 2 | 1.0 | 1.4 | 1.0 | 1b | 1 | | | | | | Dicot | Perennial forb |
| <i>Trifolium fucatum</i> | Fabaceae | WI/IN | 1.3 | 4 | 3 | 1.0 | 0.6 | 0.3 | | | | | 1 | | | Dicot | Annual forb |
| <i>Trifolium gracilentum</i> var. | Fabaceae | WI/IN | 1.0 | 3.1 | 3 | 1.0 | 1.0 | 0.5 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Annual forb |
| <i>gracilentum</i> | | | | | | | | | | | | | | | | | |
| <i>Trifolium longipes</i> var. <i>elmeri</i> | Fabaceae | BE | 5.3 | 21 | 4 | 6.0 | 1.5 | 0.8 | | 1 | 1 | | | | | Dicot | Perennial forb |
| <i>Trifolium longipes</i> var. | Fabaceae | BE/SI | 4.0 | 12 | 3 | 4.0 | 2.0 | 1.2 | | 1 | 1 | | | | | Dicot | Perennial forb |
| <i>oreganum</i> | | | | | | | | | | | | | | | | | |
| <i>Trifolium microcephalum</i> | Fabaceae | WI/IN | 1.4 | 7 | 5 | 1.0 | 1.1 | 0.5 | | 1 | 1 | | | 1 | | Dicot | Annual forb |
| <i>Trifolium willdenovii</i> | Fabaceae | WI/IN | 1.3 | 4 | 3 | 1.0 | 0.6 | 0.3 | | 1 | 1 | 1 | 1 | 1 | | Dicot | Annual forb |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | | Tax. Cat. ¹⁰ | | Lifeform ¹¹ |
|--|-----------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|---|--|----------------------------|---------|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | | | | |
| <i>Lithocarpus densiflorus</i> var. <i>echinoides</i> | Fagaceae | SI | 2.5 | 12.25 | 5 | 1.0 | 2.5 | 1.1 | | 1 | | | | | 1 | | | Dicot | Shrub |
| <i>Quercus durata</i> var. <i>durata</i> | Fagaceae | SE | 5.8 | 40.5 | 7 | 6.0 | 0.8 | 0.3 | | | | | | | | | | Dicot | Shrub |
| <i>Quercus vaccinifolia</i> | Fagaceae | SI | 2.5 | 12.25 | 5 | 2.0 | 2.2 | 1.0 | | 1 | 1 | 1 | 1 | 1 | | | | Dicot | Shrub |
| <i>Garrya buxifolia</i> | Garryaceae | SE | 5.8 | 29 | 5 | 6.0 | 0.4 | 0.2 | | 1 | 1 | | | | | | | Dicot | Shrub |
| <i>Garrya congdonii</i> | Garryaceae | BE | 5.0 | 30 | 6 | 5.5 | 1.3 | 0.5 | | 1 | 1 | 1 | | | | | | Dicot | Shrub |
| <i>Centaurium tricanthum</i> | Gentianaceae | SE | 5.5 | 11 | 2 | 5.5 | 0.7 | 0.5 | | 1 | 1 | | | | | | | Dicot | Annual forb |
| <i>Gentiana setigera</i> | Gentianaceae | SE | 5.8 | 17.5 | 3 | 6.0 | 0.3 | 0.2 | | 1 | 1 | | | | | | | Dicot | Perennial forb |
| <i>Sweritia fastigiata</i> | Gentianaceae | WI | 1.5 | 3 | 2 | 1.5 | 2.1 | 1.5 | | 1 | | | | | | | | Dicot | Perennial forb |
| <i>Emmenanthe penduliflora</i> var. <i>penduliflora</i> | Hydrophyllaceae | WI | 1.8 | 7 | 4 | 2.0 | 0.5 | 0.3 | | | 1 | 1 | 1 | 1 | | | | Dicot | Annual forb |
| <i>Emmenanthe penduliflora</i> var. <i>rosea</i> | Hydrophyllaceae | BE/SI | 4.3 | 17 | 4 | 4.5 | 1.7 | 0.9 | | | 1 | 1 | | | | | | Dicot | Annual forb |
| <i>Phacelia breweri</i> | Hydrophyllaceae | SE | 5.5 | 11 | 2 | 5.5 | 0.7 | 0.5 | | | | | | | | | | Dicot | Annual forb |
| <i>Phacelia californica</i> | Hydrophyllaceae | WI/IN | 1.4 | 4.25 | 3 | 1.0 | 1.4 | 0.8 | | | 1 | 1 | 1 | | | | | Dicot | Perennial forb |
| <i>Phacelia corymbosa</i> | Hydrophyllaceae | SE | 5.5 | 33 | 6 | 6.0 | 0.8 | 0.3 | | 1 | 1 | | | | | | | Dicot | Perennial forb |
| <i>Phacelia daleisiana</i> | Hydrophyllaceae | SE | 6.1 | 30.5 | 5 | 6.0 | 0.0 | 0.0 | 4 | 1 | | | | | | | | Dicot | Perennial forb |
| <i>Phacelia distans</i> | Hydrophyllaceae | WI/IN | 1.1 | 2.1 | 2 | 1.1 | 1.3 | 1.0 | | | 1 | 1 | 1 | | | | | Dicot | Annual forb |
| <i>Phacelia divaricata</i> | Hydrophyllaceae | WI | 2.3 | 7 | 3 | 3.0 | 1.2 | 0.7 | | | 1 | 1 | 1 | | | | | Dicot | Annual forb |
| <i>Phacelia egneri</i> | Hydrophyllaceae | WI | 2.1 | 6.25 | 3 | 3.0 | 1.6 | 0.9 | | 1 | 1 | 1 | 1 | 1 | | | | Dicot | Perennial forb |
| <i>Phacelia greenii</i> | Hydrophyllaceae | SE | 6.1 | 36.5 | 6 | 6.0 | 0.0 | 0.0 | 1b | 1 | | | | | | | | Dicot | Annual forb |
| <i>Phacelia imbricata</i> ssp. <i>imbricata</i> | Hydrophyllaceae | WI | 1.7 | 5 | 3 | 1.0 | 1.2 | 0.7 | | | 1 | 1 | 1 | 1 | | | | Dicot | Perennial forb |
| <i>Phacelia leonis</i> | Hydrophyllaceae | BE/SI | 3.9 | 27.5 | 7 | 4.0 | 1.1 | 0.4 | 1b | 1 | | | | | | | | Dicot | Annual forb |
| <i>Phacelia phacelioides</i> | Hydrophyllaceae | BE/SI | 4.2 | 12.5 | 3 | 6.0 | 3.2 | 1.8 | | | 1 | 1 | | | | | | Dicot | Annual forb |
| <i>Phacelia pringlei</i> | Hydrophyllaceae | BE/SI | 4.0 | 12 | 3 | 4.0 | 1.0 | 0.6 | | 1 | | | | | | | | Dicot | Annual forb |
| <i>Phacelia purpusii</i> | Hydrophyllaceae | WI/IN | 1.1 | 2.1 | 2 | 1.1 | 1.3 | 1.0 | | | | | | 1 | | | | Dicot | Annual forb |
| <i>Iris bracteata</i> | Iridaceae | SE | 5.8 | 11.5 | 2 | 5.5 | 0.7 | 0.5 | 3 | 1 | | | | | | | | Monocot | Perennial forb (rhiz.) |
| <i>Iris innominata</i> | Iridaceae | SE | 5.8 | 11.5 | 2 | 5.5 | 0.7 | 0.5 | 4 | 1 | 1 | | | | | | | Monocot | Perennial forb (rhiz.) |
| <i>Iris macrosiphon</i> | Iridaceae | WI/IN | 1.1 | 3.25 | 3 | 1.0 | 0.9 | 0.5 | | | 1 | 1 | | 1 | | | | Monocot | Perennial forb (rhiz.) |
| <i>Iris tenuissima</i> ssp. <i>purdyiformis</i> | Iridaceae | WI | 1.5 | 3 | 2 | 1.5 | 2.1 | 1.5 | | 1 | | | | | 1 | | | Monocot | Perennial forb (rhiz.) |
| <i>Acanthomintha duttonii</i> | Lamiaceae | SE | 6.1 | 30.5 | 5 | 6.0 | 0.0 | 0.0 | 1b | | | | | 1 | 1 | | | Dicot | Annual forb |
| <i>Acanthomintha ilicifolia</i> | Lamiaceae | WI/IN | 1.3 | 3 | 3 | 0.0 | 1.7 | 1.0 | | | | | | 1 | | | | Dicot | Annual forb |
| <i>Acanthomintha lanceolata</i> | Lamiaceae | SI | 3.4 | 16.75 | 5 | 3.0 | 2.1 | 0.9 | 4 | | | | 1 | 1 | | | | Dicot | Annual forb |
| <i>Acanthomintha obovata</i> ssp. <i>obovata</i> | Lamiaceae | BE/SI | 3.5 | 10.5 | 3 | 3.0 | 2.5 | 1.5 | 4 | | | | | 1 | | | | Dicot | Annual forb |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|--|------------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|--|-------------------------|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | | |
| <i>Monardella antonina</i> ssp. <i>benitensis</i> <i>Monardella douglasii</i> ssp. <i>douglasii</i> <i>Monardella follettii</i> <i>Monardella palmeri</i> | Lamiaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 4 | | 1 | | | | | Dicot | Perennial forb (rhiz.) |
| | Lamiaceae | SI | 3.0 | 6 | 2 | 3.0 | 1.4 | 1.0 | | 1 | 1 | 1 | | | | Dicot | Annual forb |
| | Lamiaceae | SE | 5.8 | 34.5 | 6 | 6.0 | 0.8 | 0.3 | 1b | | | | 1 | | | Dicot | Shrub |
| | Lamiaceae | BE | 4.8 | 28.5 | 6 | 6.0 | 2.2 | 0.9 | 1b | | | 1 | | | | Dicot | Perennial forb (rhiz.) |
| <i>Monardella purpurea</i> <i>Monardella sheltonii</i> <i>Monardella stebbinsii</i> | Lamiaceae | BE/SI | 4.4 | 22 | 5 | 6.0 | 2.3 | 1.0 | | 1 | 1 | 1 | 1 | | | Dicot | Perennial forb |
| | Lamiaceae | SI | 3.0 | 18 | 6 | 3.0 | 1.7 | 0.7 | | 1 | 1 | | | 1 | | Dicot | Perennial forb |
| | Lamiaceae | SE | 6.1 | 30.5 | 5 | 6.0 | 0.0 | 0.0 | 1b | | | | | 1 | | Dicot | Perennial forb (rhiz.) |
| | Lamiaceae | BE/SI | 4.3 | 17 | 4 | 4.5 | 2.1 | 1.0 | | | 1 | | | | | Dicot | Perennial forb |
| <i>Salvia sonomensis</i> <i>Scutellaria antirrhinoides</i> <i>Stachys pycnantha</i> <i>Trichostema laxum</i> <i>Trichostema rubisepalum</i> <i>Pinguicula vulgaris</i> ssp. <i>macroceras</i> <i>Allium acuminatum</i> <i>Allium amplexens</i> <i>Allium bolanderi</i> var. <i>bolanderi</i> <i>Allium bolanderi</i> var. <i>mirabile</i> <i>Allium cratericola</i> <i>Allium crispum</i> <i>Allium diabloense</i> <i>Allium falcifolium</i> <i>Allium fimbriatum</i> var. <i>purdyi</i> <i>Allium hoffmanii</i> <i>Allium howellii</i> var. <i>sanbenitense</i> | Lamiaceae | WI | 1.6 | 9.5 | 6 | 1.5 | 1.3 | 0.5 | | 1 | 1 | 1 | 1 | | | Dicot | Shrub |
| | Lamiaceae | WI | 2.3 | 11.5 | 5 | 3.0 | 1.5 | 0.7 | | 1 | 1 | | | 1 | | Dicot | Perennial forb |
| | Lamiaceae | WI | 2.2 | 11 | 5 | 1.0 | 2.4 | 1.1 | | 1 | 1 | 1 | 1 | | | Dicot | Perennial forb |
| | Lamiaceae | BE/SI | 4.0 | 16 | 4 | 4.5 | 2.4 | 1.2 | | 1 | 1 | | | 1 | | Dicot | Annual forb |
| | Lamiaceae | BE | 5.4 | 21.5 | 4 | 6.0 | 1.5 | 0.8 | 4 | | 1 | 1 | 1 | | | Dicot | Annual forb |
| | Lentibulariaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 2 | 1 | | | | | | Dicot | Perennial forb (carn.) |
| | Liliaceae | WI | 1.5 | 4.5 | 3 | 2.0 | 0.9 | 0.5 | | 1 | 1 | 1 | | | | Monocot | Perennial forb (bulb) |
| | Liliaceae | WI | 2.3 | 11.25 | 5 | 2.0 | 2.2 | 1.0 | | 1 | 1 | 1 | 1 | | | Monocot | Perennial forb (bulb) |
| | Liliaceae | WI/IN | 1.1 | 4.5 | 4 | 1.0 | 0.6 | 0.3 | | 1 | 1 | 1 | | | | Monocot | Perennial forb (bulb) |
| | Liliaceae | WI | 2.0 | 4 | 2 | 2.0 | 0.0 | 0.0 | | 1 | 1 | | | | | Monocot | Perennial forb (bulb) |
| <i>Allium cratericola</i> <i>Allium crispum</i> <i>Allium diabloense</i> <i>Allium falcifolium</i> <i>Allium fimbriatum</i> var. <i>purdyi</i> <i>Allium hoffmanii</i> <i>Allium howellii</i> var. <i>sanbenitense</i> | Liliaceae | SI | 2.6 | 15.75 | 6 | 2.5 | 1.9 | 0.8 | | 1 | 1 | | | 1 | | Monocot | Perennial forb (bulb) |
| | Liliaceae | WI/IN | 1.3 | 3.75 | 3 | 1.0 | 0.7 | 0.4 | | | 1 | 1 | 1 | | | Monocot | Perennial forb (bulb) |
| | Liliaceae | SE | 6.0 | 18 | 3 | 6.0 | 0.0 | 0.0 | | | | | 1 | | | Monocot | Perennial forb (bulb) |
| | Liliaceae | BE/SI | 4.2 | 38 | 9 | 4.0 | 1.6 | 0.5 | | 1 | 1 | 1 | | | | Monocot | Perennial forb (bulb) |
| | Liliaceae | BE | 5.4 | 21.5 | 4 | 6.0 | 1.5 | 0.8 | 4 | | 1 | | | | | Monocot | Perennial forb (bulb) |
| | Liliaceae | SE | 6.1 | 30.5 | 5 | 6.0 | 0.0 | 0.0 | 4 | 1 | 1 | | | | | Monocot | Perennial forb (bulb) |
| | Liliaceae | BE/SI | 4.0 | 12 | 3 | 4.0 | 1.0 | 0.6 | | | | | | 1 | | Monocot | Perennial forb (bulb) |
| | Liliaceae | WI | 1.5 | 4.5 | 3 | 2.0 | 0.9 | 0.5 | | 1 | 1 | 1 | | | | Monocot | Perennial forb (bulb) |
| | Liliaceae | WI | 2.3 | 11.25 | 5 | 2.0 | 2.2 | 1.0 | | 1 | 1 | 1 | 1 | | | Monocot | Perennial forb (bulb) |
| | Liliaceae | WI/IN | 1.1 | 4.5 | 4 | 1.0 | 0.6 | 0.3 | | 1 | 1 | 1 | | | | Monocot | Perennial forb (bulb) |

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Geog. Dist. ⁹ | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|---|-----------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|--------------------------|----|----|----|----|-------------------------|------------------------|
| | | | | | | | | | KL | NC | BA | SC | SN | | |
| <i>Allium jepsonii</i> | Liliaceae | BE | 5.4 | 37.5 | 7 | 6.0 | 1.0 | 0.4 | 1b | | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Allium lacunosum</i> var. <i>lacunosum</i> | Liliaceae | BE/SI | 3.8 | 15.25 | 4 | 4.5 | 2.8 | 1.4 | | 1 | 1 | | | Monocot | Perennial forb (bulb) |
| <i>Allium lacunosum</i> var. <i>micranthum</i> | Liliaceae | BE/SI | 4.3 | 13 | 3 | 6.0 | 2.9 | 1.7 | | | | 1 | | Monocot | Perennial forb (bulb) |
| <i>Allium membranaceum</i> | Liliaceae | WI/IN | 1.3 | 4 | 3 | 1.0 | 1.5 | 0.9 | | 1 | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Allium obtusum</i> var. <i>conspicuum</i> | Liliaceae | WI/IN | 1.0 | 2 | 2 | 1.0 | 1.4 | 1.0 | | | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Allium peninsulare</i> var. <i>franciscanum</i> | Liliaceae | WI | 1.8 | 3.5 | 2 | 1.8 | 1.8 | 1.3 | 1b | | 1 | 1 | | Monocot | Perennial forb (bulb) |
| <i>Allium sanbornii</i> var. <i>congdonii</i> | Liliaceae | SE | 5.6 | 22.5 | 4 | 6.0 | 1.0 | 0.5 | 4 | | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Allium sanbornii</i> var. <i>sanbornii</i> | Liliaceae | SI | 3.4 | 27 | 8 | 3.5 | 2.2 | 0.8 | 4 | | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Allium serra</i> | Liliaceae | SI | 2.6 | 10.5 | 4 | 3.0 | 1.5 | 0.7 | | 1 | 1 | 1 | | Monocot | Perennial forb (bulb) |
| <i>Allium sharsmithiae</i> | Liliaceae | BE | 5.1 | 20.5 | 4 | 6.0 | 2.0 | 1.0 | 1b | | 1 | 1 | | Monocot | Perennial forb (bulb) |
| <i>Allium siskiyouense</i> | Liliaceae | SI | 2.8 | 14 | 5 | 2.0 | 1.8 | 0.8 | 4 | 1 | 1 | | | Monocot | Perennial forb (bulb) |
| <i>Allium tuolumnense</i> | Liliaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Allium unifolium</i> | Liliaceae | WI/IN | 1.0 | 3 | 3 | 1.0 | 1.0 | 0.6 | | 1 | 1 | 1 | | Monocot | Perennial forb (bulb) |
| <i>Brodiaea californica</i> var. <i>californica</i> | Liliaceae | WI/IN | 1.1 | 4.5 | 4 | 1.3 | 1.0 | 0.5 | | 1 | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Brodiaea californica</i> var. <i>leptandra</i> | Liliaceae | WI | 2.0 | 4 | 2 | 2.0 | 1.4 | 1.0 | | 1 | | | | Monocot | Perennial forb |
| <i>Brodiaea coronaria</i> ssp. <i>coronaria</i> | Liliaceae | WI/IN | 1.0 | 2 | 2 | 1.0 | 1.4 | 1.0 | | 1 | 1 | | 1 | Monocot | Perennial forb |
| <i>Brodiaea coronaria</i> ssp. <i>rosea</i> | Liliaceae | SE | 5.5 | 27.5 | 5 | 6.0 | 1.3 | 0.6 | 1b | | | | | Monocot | Perennial forb |
| <i>Brodiaea pallida</i> | Liliaceae | BE | 4.9 | 19.5 | 4 | 5.0 | 1.5 | 0.8 | 1b | | | | 1 | Monocot | Perennial forb |
| <i>Brodiaea purdyi</i> | Liliaceae | WI | 2.2 | 11 | 5 | 2.0 | 0.8 | 0.4 | | | | | 1 | Monocot | Perennial forb |
| <i>Brodiaea stellaris</i> | Liliaceae | SE | 6.0 | 18 | 3 | 6.0 | 0.0 | 0.0 | | 1 | | | | Monocot | Perennial forb |
| <i>Calochortus clavatus</i> var. <i>clavatus</i> | Liliaceae | BE | 4.5 | 13.5 | 3 | 4.0 | 0.6 | 0.3 | 4 | | | 1 | | Monocot | Perennial forb (bulb) |
| <i>Calochortus coeruleus</i> var. <i>fimbriatus</i> | Liliaceae | WI | 1.5 | 4.5 | 3 | 1.0 | 1.3 | 0.8 | | 1 | 1 | | 1 | Monocot | Perennial forb (bulb) |
| <i>Calochortus elegans</i> var. <i>nanus</i> | Liliaceae | WI | 2.0 | 4 | 2 | 2.0 | 1.4 | 1.0 | | | | 1 | | Monocot | Perennial forb (bulb) |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Geog. Dist. ⁹ | | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|--|-----------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|--------------------------|----|----|----|----|----|-------------------------|------------------------|
| | | | | | | | | | Rarity ⁸ | KL | NC | BA | SC | SN | | |
| <i>Calochortus greenei</i> | Liliaceae | SE | 6.0 | 12 | 2 | 6.0 | 0.0 | 0.0 | 1 | | | | | | Monocot | Perennial forb (bulb) |
| <i>Calochortus nudus</i> | Liliaceae | WI | 2.1 | 8.5 | 4 | 2.5 | 1.2 | 0.6 | 1 | | | | 1 | | Monocot | Perennial forb (bulb) |
| <i>Calochortus obispoensis</i> | Liliaceae | BE | 5.4 | 21.5 | 4 | 6.0 | 1.5 | 0.8 | 1b | | | | 1 | | Monocot | Perennial forb (bulb) |
| <i>Calochortus raichei</i> | Liliaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | 1 | | | | | Monocot | Perennial forb (bulb) |
| <i>Calochortus tiburonensis</i> | Liliaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | 1 | 1 | | | | Monocot | Perennial forb (bulb) |
| <i>Calochortus umbellatus</i> | Liliaceae | SI | 2.9 | 14.5 | 5 | 3.0 | 1.1 | 0.5 | 4 | 1 | 1 | | | | Monocot | Perennial forb (bulb) |
| <i>Calochortus uniflorus</i> | Liliaceae | WI | 1.7 | 5 | 3 | 1.0 | 1.2 | 0.7 | 1 | 1 | 1 | 1 | | | Monocot | Perennial forb (bulb) |
| <i>Calochortus vestae</i> | Liliaceae | WI | 2.0 | 6 | 3 | 2.0 | 1.0 | 0.6 | 1 | 1 | | | | | Monocot | Perennial forb (bulb) |
| <i>Calochortus weedii</i> var. <i>vestus</i> | Liliaceae | WI/IN | 1.0 | 3 | 3 | 0.0 | 1.7 | 1.0 | 1b | | | 1 | | | Monocot | Perennial forb (bulb) |
| <i>Chlorogalum angustifolium</i> | Liliaceae | WI | 2.4 | 9.5 | 4 | 1.8 | 2.8 | 1.4 | | 1 | | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Chlorogalum grandiflorum</i> | Liliaceae | BE | 5.2 | 26 | 5 | 6.0 | 1.1 | 0.5 | 1b | | | | 1 | | Monocot | Perennial forb (bulb) |
| <i>Chlorogalum pomeridianum</i> var. <i>minus</i> | Liliaceae | SE | 6.1 | 30.5 | 5 | 6.0 | 0.0 | 0.0 | 1b | 1 | 1 | 1 | | | Monocot | Perennial forb (bulb) |
| <i>Chlorogalum purpureum</i> var. <i>reductum</i> | Liliaceae | SE | 5.5 | 16.5 | 3 | 6.0 | 1.2 | 0.7 | 1b | | | | 1 | | Monocot | Perennial forb (bulb) |
| <i>Erythronium californicum</i> | Liliaceae | SI | 2.7 | 8 | 3 | 2.0 | 2.1 | 1.2 | | 1 | 1 | | | | Monocot | Perennial forb (bulb) |
| <i>Erythronium citrinum</i> var. <i>citrinum</i> | Liliaceae | BE/SI | 4.3 | 21.5 | 5 | 4.0 | 0.4 | 0.2 | 4 | 1 | | | | | Monocot | Perennial forb (bulb) |
| <i>Erythronium citrinum</i> var. <i>roderickii</i> | Liliaceae | BE | 4.7 | 37.5 | 8 | 4.5 | 1.4 | 0.5 | 1b | 1 | | | | | Monocot | Perennial forb (bulb) |
| <i>Erythronium helenae</i> | Liliaceae | BE | 4.5 | 18 | 4 | 4.5 | 1.7 | 0.9 | 4 | | 1 | | | | Monocot | Perennial forb (bulb) |
| <i>Erythronium hendersonii</i> | Liliaceae | SI | 2.5 | 5 | 2 | 2.5 | 3.5 | 2.5 | | 1 | | | | | Monocot | Perennial forb (bulb) |
| <i>Erythronium howellii</i> | Liliaceae | WI | 2.3 | 7 | 3 | 2.0 | 2.5 | 1.5 | 1b | 1 | | | | | Monocot | Perennial forb (bulb) |
| <i>Erythronium multiscapoideum</i> | Liliaceae | SI | 3.0 | 15 | 5 | 2.0 | 1.7 | 0.8 | | | | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Erythronium purpurascens</i> | Liliaceae | WI/IN | 1.0 | 2 | 2 | 1.0 | 1.4 | 1.0 | | | | | | 1 | Monocot | Perennial forb (bulb) |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|--|-----------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|-------------------------|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | |
| <i>Erythronium tuolummense</i> | Liliaceae | SI | 2.5 | 5 | 2 | 2.5 | 3.5 | 2.5 | | | | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Fritillaria affinis</i> var. <i>affinis</i> | Liliaceae | WI | 2.0 | 6 | 3 | 2.0 | 0.0 | 0.0 | | 1 | 1 | 1 | | 1 | Monocot | Perennial forb (bulb) |
| <i>Fritillaria agrestis</i> | Liliaceae | SI | 2.7 | 13.25 | 5 | 2.0 | 1.6 | 0.7 | 4 | 1 | 1 | 1 | 1 | 1 | Monocot | Perennial forb (bulb) |
| <i>Fritillaria biflora</i> var. <i>biflora</i> | Liliaceae | WI | 2.3 | 9 | 4 | 2.5 | 1.7 | 0.9 | | 1 | 1 | 1 | 1 | | Monocot | Perennial forb (bulb) |
| <i>Fritillaria biflora</i> var. <i>ineziana</i> | Liliaceae | BE | 5.4 | 21.5 | 4 | 6.0 | 1.5 | 0.8 | 1b | | | 1 | | | Monocot | Perennial forb (bulb) |
| <i>Fritillaria eastwoodiae</i> | Liliaceae | WI | 2.3 | 13.5 | 6 | 2.0 | 0.4 | 0.2 | 3 | | | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Fritillaria falcata</i> | Liliaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | 1 | 1 | | Monocot | Perennial forb (bulb) |
| <i>Fritillaria glauca</i> | Liliaceae | BE/SI | 4.3 | 17.25 | 4 | 5.5 | 2.7 | 1.4 | | 1 | 1 | | | | Monocot | Perennial forb (bulb) |
| <i>Fritillaria liliacea</i> | Liliaceae | WI | 1.8 | 7 | 4 | 1.5 | 1.1 | 0.6 | 1b | | | 1 | 1 | | Monocot | Perennial forb (bulb) |
| <i>Fritillaria pluriflora</i> | Liliaceae | WI | 2.4 | 9.5 | 4 | 2.5 | 1.5 | 0.7 | | 1 | | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Fritillaria purdyi</i> | Liliaceae | BE | 4.5 | 31.5 | 7 | 4.0 | 1.8 | 0.7 | 4 | 1 | 1 | | | | Monocot | Perennial forb (bulb) |
| <i>Fritillaria recurva</i> var. <i>coccinea</i> | Liliaceae | SI | 2.7 | 8 | 3 | 2.0 | 3.1 | 1.8 | | | 1 | | | | Monocot | Perennial forb (bulb) |
| <i>Fritillaria recurva</i> var. <i>recurva</i> | Liliaceae | SI | 2.7 | 8 | 3 | 3.0 | 0.6 | 0.3 | | 1 | 1 | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Fritillaria viridea</i> | Liliaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | | | | 1 | | Monocot | Perennial forb (bulb) |
| <i>Hastingsia alba</i> | Liliaceae | SI | 3.4 | 17 | 5 | 3.0 | 1.5 | 0.7 | | 1 | 1 | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Hastingsia serpentinicola</i> | Liliaceae | SE | 6.0 | 18 | 3 | 6.0 | 0.0 | 0.0 | | 1 | 1 | | | | Monocot | Perennial forb (bulb) |
| <i>Lilium bolanderi</i> | Liliaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 4 | 1 | | | | | Monocot | Perennial forb (bulb) |
| <i>Lilium kelloggii</i> | Liliaceae | SI | 2.5 | 10 | 4 | 2.0 | 1.9 | 1.0 | | 1 | 1 | | | | Monocot | Perennial forb (bulb) |
| <i>Lilium rubescens</i> | Liliaceae | WI | 2.0 | 9.75 | 5 | 2.0 | 1.4 | 0.6 | 4 | 1 | 1 | 1 | | | Monocot | Perennial forb (bulb) |
| <i>Lilium washingtonianum</i> ssp. <i>purpurascens</i> | Liliaceae | BE/SI | 3.5 | 10.5 | 3 | 3.0 | 2.5 | 1.5 | 4 | 1 | | | | | Monocot | Perennial forb (bulb) |
| <i>Muilla maritima</i> | Liliaceae | WI | 2.0 | 6 | 3 | 2.0 | 1.0 | 0.6 | | | | 1 | 1 | 1 | Monocot | Perennial forb (bulb) |
| <i>Odontostomum hartwegii</i> | Liliaceae | SI | 2.7 | 8 | 3 | 3.0 | 0.6 | 0.3 | | 1 | | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Triteleia bridgesii</i> | Liliaceae | SI | 3.3 | 13 | 4 | 3.5 | 1.7 | 0.9 | | 1 | 1 | | | 1 | Monocot | Perennial forb (bulb) |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ | |
|---|---|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|---------|----------------------------|------------------------|-------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | | | |
| <i>Triteleia crocea</i> var. <i>crocea</i> <i>Triteleia crocea</i> var. <i>modesta</i> <i>Triteleia ixioides</i> ssp. <i>cookii</i> | Liliaceae | SI | 3.3 | 10 | 3 | 3.0 | 2.5 | 1.5 | 4 | 1 | | | | | Monocot | Perennial forb | | |
| | Liliaceae | BE | 4.5 | 22.5 | 5 | 4.0 | 1.5 | 0.7 | 4 | 1 | | | | | Monocot | Perennial forb | | |
| | Liliaceae | BE | 4.5 | 13.5 | 3 | 6.0 | 2.9 | 1.7 | 1b | | | | 1 | | Monocot | Perennial forb | | |
| <i>Triteleia peduncularis</i> <i>Xerophyllum tenax</i> | Liliaceae | BE/SI | 3.8 | 19 | 5 | 3.0 | 2.2 | 1.0 | | 1 | 1 | 1 | 1 | | Monocot | Perennial forb | | |
| | Liliaceae | WI | 1.6 | 8 | 5 | 1.0 | 0.9 | 0.4 | | 1 | 1 | 1 | 1 | 1 | Monocot | Perennial forb (rhiz.) | | |
| <i>Zigadenus micranthus</i> var. <i>fontanus</i> <i>Zigadenus paniculatus</i> | Liliaceae | BE/SI | 3.8 | 23 | 6 | 4.0 | 0.8 | 0.3 | 4 | 1 | 1 | 1 | 1 | | Monocot | Perennial forb (bulb) | | |
| | Liliaceae | WI | 1.6 | 4.75 | 3 | 2.0 | 0.7 | 0.4 | | 1 | 1 | | | 1 | Monocot | Perennial forb (bulb) | | |
| <i>Hesperolinon adenophyllum</i> <i>Hesperolinon bicarpellatum</i> <i>Hesperolinon breweri</i> <i>Hesperolinon californicum</i> <i>Hesperolinon clevelandii</i> <i>Hesperolinon congestum</i> <i>Hesperolinon didymocarpum</i> <i>Hesperolinon disjunctum</i> <i>Hesperolinon drymarioides</i> <i>Hesperolinon micranthum</i> <i>Hesperolinon serpentinum</i> <i>Hesperolinon spergulinum</i> <i>Hesperolinon tehameense</i> <i>Linum lewisii</i> <i>Sidalcea diploscypha</i> <i>Sidalcea hartwegii</i> <i>Sidalcea hickmanii</i> ssp. <i>anomala</i> <i>Sidalcea hickmanii</i> ssp. <i>viridis</i> <i>Sidalcea keckii</i> <i>Camissonia benitensis</i> <i>Camissonia lacustris</i> <i>Clarkia arcuata</i> <i>Clarkia biloba</i> ssp. <i>biloba</i> <i>Clarkia breweri</i> <i>Clarkia franciscana</i> <i>Clarkia gracilis</i> ssp. <i>albicaulis</i> <i>Clarkia gracilis</i> ssp. <i>tracyi</i> <i>Epilobium minutum</i> <i>Epilobium oregonum</i> | Linaceae | SE | 5.7 | 28.5 | 5 | 6.0 | 0.9 | 0.4 | 1b | | | | | | Dicot | Annual forb | | |
| | Linaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | | | | | | | Dicot | Annual forb | |
| | Linaceae | SI | 2.5 | 10 | 4 | 2.5 | 1.5 | 0.7 | 1b | | | 1 | | | | Dicot | Annual forb | |
| | Linaceae | SI | 2.8 | 8.5 | 3 | 3.0 | 0.6 | 0.3 | | | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| | Linaceae | WI | 2.0 | 8 | 4 | 2.0 | 1.8 | 0.9 | | | 1 | 1 | | | | Dicot | Annual forb | |
| | Linaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | 1 | 1 | | | Dicot | Annual forb | |
| | Linaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | | | 1 | | | | Dicot | Annual forb | |
| | Linaceae | SE | 6.0 | 18 | 3 | 6.0 | 0.0 | 0.0 | | | 1 | 1 | 1 | | | Dicot | Annual forb | |
| | Linaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | 1 | | | | Dicot | Annual forb | |
| | Linaceae | WI | 2.4 | 11.75 | 5 | 3.0 | 1.0 | 0.4 | | | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| | Linaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | | | | | | | Dicot | Annual forb | |
| | Linaceae | BE | 4.7 | 14 | 3 | 6.0 | 2.3 | 1.3 | | | 1 | 1 | | | | Dicot | Annual forb | |
| | Linaceae | SE | 5.8 | 34.5 | 6 | 6.0 | 0.8 | 0.3 | 1b | | | | | | | Dicot | Annual forb | |
| | Linaceae | WI/IN | 1.3 | 4 | 3 | 1.0 | 1.5 | 0.9 | | | 1 | 1 | 1 | 1 | | Dicot | Perennial forb | |
| | Malvaceae | SI | 2.6 | 13 | 5 | 3.0 | 2.3 | 1.0 | | | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| | Malvaceae | WI | 1.6 | 4.75 | 3 | 2.0 | 0.7 | 0.4 | | | 1 | | | | 1 | Dicot | Annual forb | |
| | Malvaceae | SE | 5.6 | 22.5 | 4 | 6.0 | 1.0 | 0.5 | 1b | | | | 1 | | | Dicot | Perennial forb | |
| | <i>Sidalcea hickmanii</i> ssp. <i>viridis</i> <i>Sidalcea keckii</i> <i>Camissonia benitensis</i> <i>Camissonia lacustris</i> <i>Clarkia arcuata</i> <i>Clarkia biloba</i> ssp. <i>biloba</i> <i>Clarkia breweri</i> <i>Clarkia franciscana</i> <i>Clarkia gracilis</i> ssp. <i>albicaulis</i> <i>Clarkia gracilis</i> ssp. <i>tracyi</i> <i>Epilobium minutum</i> <i>Epilobium oregonum</i> | Malvaceae | SE | 6.3 | 12.5 | 2 | 6.0 | 0.0 | 0.0 | 1b | | | 1 | 1 | | Dicot | Perennial forb | |
| | | Malvaceae | SI | 3.0 | 6 | 2 | 3.0 | 2.8 | 2.0 | 1b | | | | | 1 | | Dicot | Annual forb |
| | | Onagraceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | | 1 | | | Dicot | Annual forb |
| Onagraceae | | SI | 3.0 | 9 | 3 | 3.0 | 3.0 | 1.7 | | | 1 | | | | 1 | Dicot | Annual forb | |
| Onagraceae | | WI | 2.3 | 7 | 3 | 2.0 | 0.6 | 0.3 | | | | 1 | | | | Dicot | Annual forb | |
| Onagraceae | | WI/IN | 1.4 | 2.75 | 2 | 1.4 | 0.9 | 0.6 | | | | 1 | | | | Dicot | Annual forb | |
| Onagraceae | | BE/SI | 3.8 | 11.5 | 3 | 3.0 | 2.1 | 1.2 | 4 | | | 1 | 1 | | | Dicot | Annual forb | |
| Onagraceae | | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | 1 | 1 | | | Dicot | Annual forb | |
| Onagraceae | | WI | 2.2 | 6.5 | 3 | 2.0 | 1.0 | 0.6 | 1b | | | | | 1 | | Dicot | Annual forb | |
| Onagraceae | | BE | 5.0 | 25 | 5 | 5.0 | 1.0 | 0.4 | 4 | | | 1 | | | | Dicot | Annual forb | |
| Onagraceae | | WI | 2.0 | 6 | 3 | 2.0 | 1.0 | 0.6 | | | 1 | 1 | 1 | 1 | | Dicot | Annual forb | |
| Onagraceae | | BE/SI | 3.8 | 23 | 6 | 4.0 | 2.2 | 0.9 | | | 1 | 1 | | | | Dicot | Perennial forb | |

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|---|----------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|---|-------------------------|-------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | | |
| <i>Epilobium rigidum</i> | Onagraceae | BE | 5.1 | 20.5 | 4 | 6.0 | 2.0 | 1.0 | 4 | 1 | | | | | | Dicot | Perennial forb |
| <i>Epilobium siskiyouense</i> | Onagraceae | SE | 5.5 | 38.5 | 7 | 6.0 | 1.0 | 0.4 | 1b | 1 | | | | | | Dicot | Perennial forb |
| <i>Cypripedium californicum</i> | Orchidaceae | BE | 4.5 | 40.5 | 9 | 4.0 | 1.3 | 0.4 | 4 | 1 | 1 | 1 | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Cypripedium fasciculatum</i> | Orchidaceae | SI | 2.5 | 12.25 | 5 | 2.0 | 1.6 | 0.7 | 4 | 1 | 1 | 1 | | | 1 | Monocot | Perennial forb (bulb) |
| <i>Piperia candida</i> | Orchidaceae | WI/IN | 1.2 | 3.5 | 3 | 1.0 | 1.0 | 0.6 | 4 | 1 | 1 | 1 | | | | Monocot | Perennial forb (bulb) |
| <i>Orobanche valida</i> ssp. <i>howellii</i> | Orobanchaceae | SI | 3.4 | 13.5 | 4 | 3.0 | 1.3 | 0.6 | 4 | 1 | | | | | | Dicot | Perennial forb (paras.) |
| <i>Dicentra chrysantha</i> | Papaveraceae | WI/IN | 1.1 | 3.25 | 3 | 1.0 | 0.9 | 0.5 | | 1 | 1 | 1 | 1 | | 1 | Dicot | Perennial forb |
| <i>Dicentra formosa</i> ssp. <i>oregana</i> | Papaveraceae | SE | 5.6 | 22.5 | 4 | 6.0 | 1.0 | 0.5 | 4 | 1 | | | | | | Dicot | Perennial forb |
| <i>Dicentra pauciflora</i> | Papaveraceae | WI | 2.2 | 6.5 | 3 | 3.0 | 1.4 | 0.8 | | 1 | | | | | 1 | Dicot | Perennial forb |
| <i>Eschscholzia hypaeoides</i> | Papaveraceae | SI | 2.6 | 7.75 | 3 | 1.0 | 3.1 | 1.8 | 4 | | | 1 | | | | Dicot | Annual forb |
| <i>Platystemon californicus</i> | Papaveraceae | WI | 1.7 | 5 | 3 | 2.0 | 0.6 | 0.3 | | 1 | 1 | 1 | 1 | | 1 | Dicot | Annual forb |
| <i>Picea breweriana</i> | Pinaceae | WI | 2.2 | 6.5 | 3 | 3.0 | 1.4 | 0.8 | | 1 | | | | | 1 | Gymnosp. | Tree |
| <i>Pinus attenuata</i> | Pinaceae | SI | 2.5 | 12.6 | 5 | 3.0 | 2.4 | 1.1 | | 1 | 1 | 1 | 1 | | 1 | Gymnosp. | Tree |
| <i>Pinus balfouriana</i> ssp. <i>balfouriana</i> | Pinaceae | BE/SI | 4.3 | 26 | 6 | 4.0 | 1.5 | 0.6 | | 1 | | | | | | Gymnosp. | Tree |
| <i>Pinus coulteri</i> | Pinaceae | WI/IN | 1.3 | 4 | 3 | 1.0 | 1.5 | 0.9 | | | 1 | 1 | | | | Gymnosp. | Tree |
| <i>Pinus jeffreyi</i> | Pinaceae | SI | 2.7 | 8 | 3 | 3.0 | 0.6 | 0.3 | | 1 | 1 | 1 | 1 | | 1 | Gymnosp. | Tree |
| <i>Pinus sabiniana</i> | Pinaceae | WI/IN | 1.4 | 4.25 | 3 | 1.0 | 1.4 | 0.8 | | 1 | 1 | 1 | 1 | | 1 | Gymnosp. | Tree |
| <i>Plantago erecta</i> | Plantaginaceae | WI/IN | 1.0 | 3 | 3 | 1.0 | 1.0 | 0.6 | | 1 | 1 | 1 | 1 | | 1 | Dicot | Annual forb |
| <i>Achnatherum lemmonii</i> var. <i>pubescens</i> | Poaceae | BE | 4.8 | 14.5 | 3 | 6.0 | 2.3 | 1.3 | 3 | 1 | 1 | | | | | Monocot | Perennial gram. |
| <i>Achnatherum nelsonii</i> var. <i>dorei</i> | Poaceae | WI/IN | 1.0 | 2 | 2 | 1.0 | 1.4 | 1.0 | | | | | | 1 | | Monocot | Perennial (cesp.) |
| <i>Achnatherum stillmanii</i> | Poaceae | WI/IN | 1.1 | 2.1 | 2 | 1.1 | 1.3 | 1.0 | | | | | | 1 | | Monocot | Perennial gram. |
| <i>Agrostis microphylla</i> | Poaceae | WI/IN | 1.1 | 4.25 | 4 | 1.1 | 1.1 | 0.5 | | | 1 | 1 | 1 | | | Monocot | Annual gram. |
| <i>Bromus laevipes</i> | Poaceae | WI | 1.7 | 65 | 3 | 2.0 | 0.6 | 0.3 | | 1 | 1 | 1 | 1 | | 1 | Monocot | Perennial gram. |
| <i>Calamagrostis foliosa</i> | Poaceae | WI | 1.7 | 5 | 3 | 2.0 | 1.5 | 0.9 | | 1 | | | | | | Monocot | Perennial (cesp.) |
| <i>Calamagrostis ophitidis</i> | Poaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 4 | 1 | 1 | | | | | Monocot | Perennial gram. (rhiz.) |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|--|---------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|---------|-------------------------|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | | |
| <i>Calamagrostis stricta</i> ssp. <i>inexpansa</i> | Poaceae | WI | 1.5 | 3 | 2 | 1.5 | 2.1 | 1.5 | 1 | 1 | 1 | 1 | 1 | 1 | Monocot | Perennial gram. (cesp.) | |
| <i>Danthonia californica</i> var. <i>californica</i> | Poaceae | SI | 3.3 | 13 | 4 | 3.0 | 2.2 | 1.1 | 1 | 1 | 1 | 1 | 1 | 1 | Monocot | Perennial gram. (cesp.) | |
| <i>Elymus trachycaulus</i> ssp. <i>trachycaulus</i> | Poaceae | WI | 1.6 | 3.1 | 2 | 1.6 | 2.1 | 1.5 | 1 | 1 | 1 | 1 | 1 | 1 | Monocot | Perennial gram. (cesp.) | |
| <i>Festuca californica</i> | Poaceae | WI | 2.4 | 11.75 | 5 | 2.0 | 1.6 | 0.7 | 1 | 1 | 1 | 1 | 1 | 1 | Monocot | Perennial gram. (cesp.) | |
| <i>Festuca idahoensis</i> | Poaceae | WI/IN | 1.3 | 5.25 | 4 | 1.0 | 1.2 | 0.6 | 1 | 1 | 1 | 1 | 1 | 1 | Monocot | Perennial gram. (cesp.) | |
| <i>Hordeum brachyantherum</i> ssp. <i>californicum</i> | Poaceae | SI | 3.1 | 9.25 | 3 | 3.0 | 2.9 | 1.7 | 1 | 1 | 1 | 1 | 1 | 1 | Monocot | Perennial gram. (cesp.) | |
| <i>Melica geyeri</i> | Poaceae | WI/IN | 1.2 | 6 | 5 | 1.0 | 0.4 | 0.2 | 1 | 1 | 1 | 1 | 1 | 1 | Monocot | Perennial gram. (cesp.) | |
| <i>Poa piperi</i> | Poaceae | BE | 5.4 | 21.5 | 4 | 5.5 | 1.0 | 0.5 | 4 | 1 | | | | | Monocot | Perennial gram. (cesp.) | |
| <i>Poa rhizomata</i> | Poaceae | WI | 1.8 | 3.5 | 2 | 1.5 | 2.1 | 1.5 | 4 | 1 | | | | | Monocot | Perennial gram. (rhiz.) | |
| <i>Poa tenerrima</i> | Poaceae | SI | 3.3 | 13 | 4 | 3.0 | 1.3 | 0.6 | | 1 | 1 | 1 | 1 | 1 | Monocot | Perennial gram. (cesp.) | |
| <i>Scribneria bolanderi</i> | Poaceae | WI | 1.7 | 5.1 | 3 | 1.0 | 2.0 | 1.2 | | 1 | 1 | 1 | 1 | 1 | Monocot | Annual gram. | |
| <i>Vulpia microstachys</i> var. <i>microstachys</i> | Poaceae | WI | 2.3 | 9.1 | 4 | 2.0 | 2.0 | 1.0 | 1 | 1 | 1 | 1 | 1 | 1 | Monocot | Annual gram. | |
| <i>Collomia diversifolia</i> | Polemoniaceae | SE | 5.6 | 33.5 | 6 | 6.0 | 1.2 | 0.5 | 4 | | 1 | 1 | | | Dicot | Annual forb | |
| <i>Collomia tinctoria</i> | Polemoniaceae | WI | 1.8 | 7.1 | 4 | 2.0 | 1.5 | 0.7 | | 1 | 1 | | | 1 | Dicot | Annual forb | |
| <i>Gilia capitata</i> ssp. <i>capitata</i> | Polemoniaceae | WI | 1.6 | 4.75 | 3 | 1.0 | 1.2 | 0.7 | | 1 | 1 | | | | Dicot | Annual, Perennial forb | |
| <i>Gilia sinistra</i> ssp. <i>pinnatisecta</i> | Polemoniaceae | BE/SI | 3.8 | 19 | 5 | 3.0 | 2.2 | 1.0 | 4 | | 1 | | | | Dicot | Annual, Perennial forb | |

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | | Tax. ¹⁰ | | Lifeform ¹¹ |
|---|---------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|------|-------|------------------------|--|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | Cat. | | | | |
| <i>Gilia sinistra</i> ssp. <i>sinistra</i> | Polemoniaceae | SI | 2.5 | 7.5 | 3 | 3.0 | 1.8 | 1.0 | | 1 | 1 | | | 1 | | Dicot | Annual forb | | |
| <i>Linanthus ambiguus</i> | Polemoniaceae | SE | 5.8 | 17.5 | 3 | 6.0 | 0.6 | 0.3 | 4 | | | 1 | 1 | | | Dicot | Annual forb | | |
| <i>Linanthus bolanderi</i> | Polemoniaceae | WI/IN | 1.3 | 2.5 | 2 | 1.3 | 1.1 | 0.8 | | | 1 | 1 | | 1 | | Dicot | Annual forb | | |
| <i>Linanthus dichotomus</i> | Polemoniaceae | SI | 2.5 | 12.35 | 5 | 3.0 | 2.4 | 1.1 | | 1 | 1 | 1 | 1 | | | Dicot | Annual forb | | |
| <i>Linanthus latisectus</i> (= <i>Leptosiphon</i> la.) | Polemoniaceae | WI | 2.0 | 6 | 3 | 2.0 | 0.0 | 0.0 | | | 1 | | | | | Dicot | Annual forb | | |
| <i>Linanthus liniflorus</i> (= <i>Leptosiphon</i> li.) | Polemoniaceae | WI | 1.6 | 6.25 | 4 | 1.5 | 1.2 | 0.6 | | 1 | 1 | 1 | 1 | | | Dicot | Annual forb | | |
| <i>Linanthus nuttallii</i> ssp. <i>howellii</i> (= <i>Leptosiphon</i> n. s. h.) | Polemoniaceae | BE | 5.3 | 31.5 | 6 | 6.0 | 1.3 | 0.5 | 1b | 1 | | | | | | Dicot | Perennial forb | | |
| <i>Navarretia heterodoxa</i> | Polemoniaceae | SI | 2.8 | 14 | 5 | 3.0 | 2.4 | 1.1 | | | | 1 | | | | Dicot | Annual forb | | |
| <i>Navarretia jaredii</i> | Polemoniaceae | SE | 5.9 | 23.5 | 4 | 6.0 | 0.5 | 0.3 | 4 | | | | 1 | | | Dicot | Annual forb | | |
| <i>Navarretia jepsonii</i> | Polemoniaceae | SE | 5.6 | 22.5 | 4 | 5.5 | 0.6 | 0.3 | 4 | | 1 | | | | | Dicot | Annual forb | | |
| <i>Navarretia pubescens</i> | Polemoniaceae | WI | 2.0 | 6 | 3 | 2.0 | 1.0 | 0.6 | | 1 | 1 | 1 | 1 | | | Dicot | Annual forb | | |
| <i>Navarretia rosulata</i> | Polemoniaceae | SE | 6.0 | 18 | 3 | 6.0 | 0.0 | 0.0 | 1b | | 1 | 1 | | | | Dicot | Annual forb | | |
| <i>Phlox hirsuta</i> | Polemoniaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | 1 | | | | | | Dicot | Perennial forb | | |
| <i>Polemonium chartaceum</i> | Polemoniaceae | WI | 1.6 | 8.1 | 5 | 2.0 | 1.5 | 0.7 | 1b | 1 | | | | 1 | | Dicot | Perennial forb | | |
| <i>Polygala cornuta</i> var. <i>cornuta</i> | Polygalaceae | WI | 2.3 | 9 | 4 | 2.0 | 1.3 | 0.6 | | 1 | | | | | 1 | Dicot | Perennial forb, Shrub | | |
| <i>Chorizanthe breweri</i> | Polygonaceae | BE | 5.4 | 21.5 | 4 | 5.5 | 1.0 | 0.5 | 1b | | | | 1 | | | Dicot | Annual forb | | |
| <i>Chorizanthe palmeri</i> | Polygonaceae | BE | 4.9 | 24.5 | 5 | 6.0 | 1.6 | 0.7 | 4 | | | | 1 | | | Dicot | Annual forb | | |
| <i>Chorizanthe uniaristata</i> | Polygonaceae | SI | 2.7 | 10.75 | 4 | 2.5 | 2.0 | 1.0 | | | | | 1 | 1 | | Dicot | Annual, Perennial forb | | |
| <i>Chorizanthe ventricosa</i> | Polygonaceae | BE | 5.3 | 16 | 3 | 6.0 | 1.2 | 0.7 | 4 | | | | 1 | | | Dicot | Annual forb | | |
| <i>Eriogonum alpinum</i> | Polygonaceae | SE | 6.1 | 30.5 | 5 | 6.0 | 0.0 | 0.0 | 1b | 1 | | | | | | Dicot | Perennial forb | | |
| <i>Eriogonum argillosum</i> | Polygonaceae | SI | 3.1 | 12.5 | 4 | 3.0 | 2.6 | 1.3 | 4 | | | 1 | 1 | | | Dicot | Annual forb | | |
| <i>Eriogonum compositum</i> var. <i>compositum</i> | Polygonaceae | WI | 1.7 | 5.1 | 3 | 2.0 | 1.5 | 0.9 | | 1 | 1 | | | | | Dicot | Perennial forb | | |
| <i>Eriogonum congdonii</i> | Polygonaceae | BE | 5.1 | 35.5 | 7 | 6.0 | 1.7 | 0.7 | 4 | 1 | | | | | | Dicot | Shrub | | |
| <i>Eriogonum covilleum</i> | Polygonaceae | SI | 3.0 | 12 | 4 | 3.0 | 1.6 | 0.8 | | | | | 1 | | | Dicot | Annual forb | | |
| <i>Eriogonum dasyanthemum</i> | Polygonaceae | SI | 3.0 | 6 | 2 | 3.0 | 1.4 | 1.0 | | | 1 | | | | | Dicot | Annual forb | | |
| <i>Eriogonum dclinum</i> | Polygonaceae | SI | 3.2 | 9.5 | 3 | 3.0 | 3.0 | 1.7 | 4 | 1 | | | | | | Dicot | Perennial forb | | |
| <i>Eriogonum elatum</i> var. <i>villosum</i> | Polygonaceae | SI | 3.3 | 13 | 4 | 3.5 | 3.2 | 1.6 | | 1 | | | | 1 | | Dicot | Perennial forb | | |
| <i>Eriogonum hirtellum</i> | Polygonaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | 1 | | | | | | Dicot | Perennial forb (rhiz.) | | |
| <i>Eriogonum hirtiflorum</i> | Polygonaceae | SI | 3.3 | 13 | 4 | 3.5 | 3.2 | 1.6 | | 1 | 1 | 1 | 1 | | | Dicot | Annual forb | | |
| <i>Eriogonum kelloggii</i> | Polygonaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | 1 | | | | | Dicot | Perennial forb | | |
| <i>Eriogonum libertini</i> | Polygonaceae | SE | 6.1 | 36.5 | 6 | 6.0 | 0.0 | 0.0 | 4 | 1 | 1 | | | | | Dicot | Perennial forb | | |
| <i>Eriogonum luteolum</i> var. <i>caninum</i> | Polygonaceae | SE | 5.5 | 27.5 | 5 | 6.0 | 0.9 | 0.4 | 3 | 1 | 1 | 1 | | | | Dicot | Annual forb | | |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|---|---------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|-------|-------------------------|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | | |
| <i>Eriogonum luteolum</i> var. <i>luteolum</i> | Polygonaceae | BE/SI | 3.8 | 15 | 4 | 3.0 | 1.5 | 0.8 | | 1 | 1 | 1 | | 1 | Dicot | Annual forb | |
| <i>Eriogonum nervulosum</i> | Polygonaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 1b | | | 1 | | | Dicot | Perennial forb (rhiz.) | |
| <i>Eriogonum nudum</i> var. <i>indictum</i> | Polygonaceae | WI | 1.5 | 4.5 | 3 | 1.0 | 0.6 | 0.3 | 4 | | | | 1 | | Dicot | Perennial forb | |
| <i>Eriogonum nudum</i> var. <i>oblongifolium</i> | Polygonaceae | WI | 2.0 | 6 | 3 | 2.0 | 0.0 | 0.0 | | 1 | 1 | | | 1 | Dicot | Perennial forb | |
| <i>Eriogonum pendulum</i> | Polygonaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 2 | | | | | | Dicot | Perennial forb | |
| <i>Eriogonum pyrolifolium</i> | Polygonaceae | WI/IN | 1.0 | 3 | 3 | 0.0 | 1.7 | 1.0 | | 1 | | | | 1 | Dicot | Perennial forb | |
| <i>Eriogonum siskiyouense</i> | Polygonaceae | BE | 5.4 | 32.5 | 6 | 6.0 | 1.2 | 0.5 | 4 | 1 | | | | | Dicot | Perennial forb | |
| <i>Eriogonum strictum</i> var. <i>greenii</i> | Polygonaceae | SE | 5.9 | 29.5 | 5 | 6.0 | 0.4 | 0.2 | 4 | 1 | 1 | | | | Dicot | Perennial forb | |
| <i>Eriogonum strictum</i> var. <i>proliferum</i> | Polygonaceae | SE | 6.0 | 24 | 4 | 6.0 | 0.0 | 0.0 | | 1 | 1 | | | 1 | Dicot | Perennial forb | |
| <i>Eriogonum ternatum</i> | Polygonaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 4 | 1 | 1 | | | | Dicot | Perennial forb | |
| <i>Eriogonum trichopes</i> var. <i>hooveri</i> | Polygonaceae | SI | 3.3 | 10 | 3 | 3.0 | 2.5 | 1.5 | | | | | 1 | | Dicot | Annual forb | |
| <i>Eriogonum tripodum</i> | Polygonaceae | BE | 5.3 | 26.5 | 5 | 6.0 | 1.3 | 0.6 | 4 | | | 1 | | 1 | Dicot | Shrub | |
| <i>Eriogonum umbellatum</i> var. <i>argus</i> | Polygonaceae | SI | 3.0 | 12 | 4 | 3.5 | 1.4 | 0.7 | | 1 | 1 | | | | Dicot | Perennial forb | |
| <i>Eriogonum umbellatum</i> var. <i>bahiiforme</i> | Polygonaceae | BE/SI | 3.5 | 21 | 6 | 3.0 | 1.2 | 0.5 | 4 | | 1 | 1 | 1 | | Dicot | Perennial forb | |
| <i>Eriogonum umbellatum</i> var. <i>goodmanii</i> | Polygonaceae | SI | 3.3 | 10 | 3 | 3.0 | 2.5 | 1.5 | | 1 | | | | | Dicot | Perennial forb | |
| <i>Eriogonum umbellatum</i> var. <i>humistratum</i> | Polygonaceae | BE | 4.5 | 27.25 | 6 | 5.0 | 2.1 | 0.8 | 4 | 1 | 1 | | | | Dicot | Perennial forb | |
| <i>Eriogonum umbellatum</i> var. <i>speciosum</i> | Polygonaceae | BE/SI | 4.2 | 21 | 5 | 4.0 | 1.3 | 0.6 | | 1 | | | | 1 | Dicot | Perennial forb | |
| <i>Eriogonum ursinum</i> | Polygonaceae | WI/IN | 1.1 | 2.25 | 2 | 1.1 | 1.2 | 0.9 | | 1 | | | | 1 | Dicot | Perennial forb | |
| <i>Eriogonum vinineum</i> | Polygonaceae | WI/IN | 1.0 | 3 | 3 | 1.0 | 0.0 | 0.0 | | 1 | | | | 1 | Dicot | Annual forb | |
| <i>Polygonum douglasii</i> ssp. <i>majus</i> | Polygonaceae | WI | 1.5 | 4.5 | 3 | 2.0 | 0.9 | 0.5 | | 1 | | | | 1 | Dicot | Annual forb | |
| <i>Polygonum douglasii</i> ssp. <i>spergulariiforme</i> | Polygonaceae | SI | 3.0 | 18.25 | 6 | 2.5 | 2.1 | 0.9 | | 1 | 1 | 1 | | 1 | Dicot | Annual forb | |
| <i>Systenotheca vortriedei</i> | Polygonaceae | SI | 3.1 | 12.25 | 4 | 2.5 | 2.2 | 1.1 | 4 | | | | 1 | | Dicot | Annual forb | |
| <i>Calyptridium quadripetatum</i> | Portulacaceae | BE | 4.6 | 27.5 | 6 | 4.0 | 1.2 | 0.5 | 4 | | | 1 | | | Dicot | Annual forb | |
| <i>Calyptridium umbellatum</i> | Portulacaceae | WI/IN | 1.3 | 4 | 3 | 1.0 | 1.5 | 0.9 | | 1 | 1 | 1 | | 1 | Dicot | Perennial forb | |
| <i>Claytonia exigua</i> ssp. <i>exigua</i> | Portulacaceae | SI | 3.4 | 24 | 7 | 3.0 | 1.1 | 0.4 | | 1 | 1 | 1 | 1 | 1 | Dicot | Annual forb | |
| <i>Claytonia exigua</i> ssp. <i>glauca</i> | Portulacaceae | BE/SI | 3.6 | 18 | 5 | 3.0 | 1.3 | 0.6 | | 1 | 1 | 1 | 1 | 1 | Dicot | Annual forb | |
| <i>Claytonia gypsophioides</i> | Portulacaceae | SI | 3.1 | 15.5 | 5 | 3.0 | 0.2 | 0.1 | | | | 1 | 1 | 1 | Dicot | Annual forb | |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|--|---------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|--|----------------------------|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | | |
| <i>Claytonia saxosa</i> | Portulacaceae | BE/SI | 4.4 | 21.75 | 5 | 5.0 | 2.2 | 1.0 | | 1 | 1 | | | | | Dicot | Annual forb |
| <i>Lewisia cantelovii</i> | Portulacaceae | WI/IN | 1.0 | 6 | 6 | 1.0 | 1.1 | 0.4 | 1b | 1 | | | | 1 | | Dicot | Perennial forb |
| <i>Lewisia cotyledon</i> var. <i>cotyledon</i> | Portulacaceae | WI | 2.0 | 6 | 3 | 3.0 | 1.7 | 1.0 | | 1 | | | | | | Dicot | Perennial forb |
| <i>Lewisia cotyledon</i> var. <i>heckneri</i> | Portulacaceae | WI/IN | 1.0 | 4 | 4 | 0.5 | 1.4 | 0.7 | | 1 | | | | | | Dicot | Perennial forb |
| <i>Lewisia cotyledon</i> var. <i>howellii</i> | Portulacaceae | WI/IN | 1.3 | 4 | 3 | 1.0 | 1.5 | 0.9 | | 1 | | | | | | Dicot | Perennial forb |
| <i>Lewisia leana</i> | Portulacaceae | SI | 3.0 | 6 | 2 | 3.0 | 0.0 | 0.0 | | 1 | 1 | | | 1 | | Dicot | Perennial forb |
| <i>Lewisia nevadensis</i> | Portulacaceae | WI | 1.7 | 5 | 3 | 2.0 | 1.5 | 0.9 | | 1 | 1 | | | 1 | | Dicot | Perennial forb |
| <i>Lewisia oppositifolia</i> | Portulacaceae | BE | 5.3 | 21 | 4 | 6.0 | 1.5 | 0.8 | | 1 | | | | | | Dicot | Perennial forb |
| <i>Lewisia rediviva</i> | Portulacaceae | WI/IN | 1.4 | 7 | 5 | 1.0 | 1.1 | 0.5 | | 1 | 1 | 1 | | 1 | | Dicot | Perennial forb |
| <i>Lewisia stebbinsii</i> | Portulacaceae | BE | 4.7 | 14 | 3 | 6.0 | 2.3 | 1.3 | 1b | 1 | | | | | | Dicot | Perennial forb |
| <i>Lewisia triphylla</i> | Portulacaceae | WI | 1.7 | 5 | 3 | 2.0 | 1.5 | 0.9 | | 1 | 1 | | | 1 | | Dicot | Perennial forb |
| <i>Dodecatheon clevelandii</i> ssp. <i>patulum</i> | Primulaceae | SI | 3.0 | 9 | 3 | 3.0 | 0.0 | 0.0 | | | 1 | 1 | | 1 | | Dicot | Perennial forb |
| <i>Adiantum aleuticum</i> | Pteridaceae | WI | 2.4 | 11.75 | 5 | 2.0 | 1.2 | 0.5 | | 1 | 1 | 1 | | 1 | | Pteridoph. | Perennial forb |
| <i>Aspidotis carlotta-halliae</i> | Pteridaceae | BE | 5.3 | 26.5 | 5 | 6.0 | 1.1 | 0.5 | 4 | | 1 | 1 | | 1 | | Pteridoph. | Perennial forb (rhiz.) |
| <i>Aspidotis densa</i> | Pteridaceae | SI | 3.4 | 31 | 9 | 3.0 | 1.2 | 0.4 | | 1 | 1 | 1 | | 1 | | Pteridoph. | Perennial forb |
| <i>Pellaea brachyptera</i> | Pteridaceae | WI | 1.5 | 4.5 | 3 | 2.0 | 0.9 | 0.5 | | 1 | 1 | | | 1 | | Pteridoph. | Perennial forb |
| <i>Anemone drummondii</i> | Ranunculaceae | WI | 2.3 | 6.75 | 3 | 2.0 | 1.6 | 0.9 | | 1 | | | | 1 | | Dicot | Perennial forb |
| <i>Aquilegia eximia</i> | Ranunculaceae | BE/SI | 4.2 | 25 | 6 | 3.5 | 1.5 | 0.6 | | | 1 | 1 | | 1 | | Dicot | Perennial forb |
| <i>Delphinium hesperium</i> ssp. <i>hesperium</i> | Ranunculaceae | SI | 2.7 | 8 | 3 | 3.0 | 0.6 | 0.3 | | 1 | 1 | 1 | | 1 | | Dicot | Perennial forb |
| <i>Delphinium nuttallianum</i> | Ranunculaceae | WI/IN | 1.4 | 4.1 | 3 | 1.0 | 1.5 | 0.9 | | 1 | | | | 1 | | Dicot | Perennial forb |
| <i>Delphinium parryi</i> ssp. <i>eastwoodiae</i> | Ranunculaceae | BE/SI | 3.7 | 11 | 3 | 4.0 | 2.5 | 1.5 | | | | | | 1 | | Dicot | Perennial forb |
| <i>Delphinium uliginosum</i> | Ranunculaceae | SE | 5.7 | 28.5 | 5 | 6.0 | 0.9 | 0.4 | 4 | | 1 | | | | | Dicot | Perennial forb |
| <i>Ceanothus confusus</i> | Rhamnaceae | WI/IN | 1.3 | 2.5 | 2 | 1.3 | 1.1 | 0.8 | 1b | | 1 | | | | | Dicot | Shrub |
| <i>Ceanothus cuneatus</i> var. <i>cuneatus</i> | Rhamnaceae | WI | 1.5 | 6.1 | 4 | 1.5 | 1.3 | 0.6 | | 1 | 1 | 1 | | 1 | | Dicot | Shrub |
| <i>Ceanothus divergens</i> | Rhamnaceae | WI | 2.0 | 4 | 2 | 2.0 | 1.4 | 1.0 | 1b | | 1 | | | | | Dicot | Shrub |
| <i>Ceanothus ferrisiae</i> | Rhamnaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | 1 | | | | Dicot | Shrub |
| <i>Ceanothus foliosus</i> var. <i>medius</i> | Rhamnaceae | BE/SI | 4.0 | 12 | 3 | 3.0 | 1.7 | 1.0 | | | | 1 | 1 | | | Dicot | Shrub |
| <i>Ceanothus jepsonii</i> | Rhamnaceae | SE | 6.0 | 18 | 3 | 6.0 | 0.0 | 0.0 | | | 1 | 1 | | | | Dicot | Shrub |
| <i>Ceanothus masonii</i> | Rhamnaceae | SI | 3.3 | 6.5 | 2 | 3.0 | 4.2 | 3.0 | 1b | | | 1 | | | | Dicot | Shrub |
| <i>Ceanothus papillosus</i> var. <i>roweanus</i> | Rhamnaceae | WI | 1.5 | 3 | 2 | 1.5 | 2.1 | 1.5 | | | | | | 1 | | Dicot | Shrub |
| <i>Ceanothus pumilus</i> | Rhamnaceae | SE | 5.7 | 28.5 | 5 | 6.0 | 0.9 | 0.4 | | | 1 | 1 | | | | Dicot | Shrub |
| <i>Ceanothus roderickii</i> | Rhamnaceae | WI | 1.7 | 5 | 3 | 2.0 | 1.5 | 0.9 | 1b | | | | | 1 | | Dicot | Shrub |
| <i>Ceanothus sonomensis</i> | Rhamnaceae | WI/IN | 1.3 | 4 | 3 | 2.0 | 1.2 | 0.7 | 1b | | | 1 | | | | Dicot | Shrub |

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|---|------------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|-------|------------------------|-------------------------|------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | | | |
| <i>Rhamnus californica</i> ssp. <i>occidentalis</i> | Rhamnaceae | SE | 6.0 | 24 | 4 | 6.0 | 0.0 | 0.0 | | 1 | 1 | | | 1 | Dicot | Shrub | | |
| <i>Rhamnus tomentella</i> ssp. <i>crassifolia</i> | Rhamnaceae | BE | 4.8 | 19 | 4 | 6.0 | 2.5 | 1.3 | | 1 | 1 | | | | Dicot | Shrub | | |
| <i>Rhamnus tomentella</i> ssp. <i>tomentella</i> | Rhamnaceae | WI | 1.5 | 6 | 4 | 0.8 | 1.7 | 0.8 | | 1 | 1 | 1 | 1 | 1 | Dicot | Shrub | | |
| <i>Adenostoma fasciculatum</i> | Rosaceae | WI/IN | 1.3 | 5.2 | 4 | 1.1 | 1.4 | 0.7 | | | 1 | 1 | 1 | 1 | Dicot | Shrub | | |
| <i>Holodiscus discolor</i> | Rosaceae | WI/IN | 1.0 | 3 | 3 | 1.0 | 1.0 | 0.6 | | 1 | 1 | 1 | 1 | 1 | Dicot | Shrub | | |
| <i>Horkelia congesta</i> ssp. <i>nemorosa</i> | Rosaceae | BE/SI | 3.8 | 7.5 | 2 | 3.5 | 0.7 | 0.5 | 2 | 1 | | | | | Dicot | Perennial forb | | |
| <i>Horkelia daucifolia</i> | Rosaceae | BE/SI | 3.8 | 15 | 4 | 3.0 | 1.5 | 0.8 | | 1 | 1 | | | | Dicot | Perennial forb | | |
| <i>Horkelia sericata</i> | Rosaceae | SE | 5.6 | 22.5 | 4 | 6.0 | 1.0 | 0.5 | 4 | 1 | | | | | Dicot | Perennial forb | | |
| <i>Horkelia tridentata</i> ssp. <i>flavescens</i> | Rosaceae | SI | 3.0 | 9 | 3 | 2.0 | 1.7 | 1.0 | | 1 | 1 | | | 1 | Dicot | Perennial forb | | |
| <i>Ivesia gordonii</i> | Rosaceae | WI | 1.6 | 3.25 | 2 | 1.6 | 1.9 | 1.4 | | 1 | 1 | | | 1 | Dicot | Perennial forb | | |
| <i>Ivesia pickeringii</i> | Rosaceae | BE | 5.4 | 32.5 | 6 | 6.0 | 1.0 | 0.4 | 1b | 1 | | | | | Dicot | Perennial forb | | |
| <i>Potentilla cristae</i> | Rosaceae | SI | 3.1 | 12.5 | 4 | 3.0 | 0.0 | 0.0 | 1b | 1 | | | | | Dicot | Perennial forb | | |
| <i>Sanguisorba officinalis</i> | Rosaceae | BE/SI | 4.2 | 12.5 | 3 | 3.0 | 1.7 | 1.0 | 2 | 1 | 1 | | | | Dicot | Perennial forb (rhiz.) | | |
| <i>Galium ambiguum</i> var. <i>ambiguum</i> | Rubiaceae | SI | 3.3 | 10 | 3 | 3.0 | 2.5 | 1.5 | | 1 | | | | 1 | Dicot | Perennial forb | | |
| <i>Galium ambiguum</i> var. <i>siskiyouense</i> | Rubiaceae | SE | 5.5 | 27.5 | 5 | 6.0 | 0.9 | 0.4 | | 1 | 1 | | | | Dicot | Perennial forb | | |
| <i>Galium andrewsii</i> ssp. | Rubiaceae | SI | 3.2 | 16 | 5 | 3.0 | 1.9 | 0.9 | | 1 | 1 | 1 | | | Dicot | Perennial forb | | |
| <i>Galium andrewsii</i> ssp. <i>gatense</i> | Rubiaceae | BE | 5.1 | 20.5 | 4 | 5.0 | 0.8 | 0.4 | 4 | | | 1 | 1 | | Dicot | Perennial forb | | |
| <i>Galium andrewsii</i> ssp. <i>intermedium</i> | Rubiaceae | WI/IN | 1.4 | 2.75 | 2 | 1.4 | 0.9 | 0.6 | | | | | 1 | | Dicot | Perennial forb | | |
| <i>Galium clementis</i> | Rubiaceae | WI/IN | 1.0 | 2 | 2 | 1.0 | 1.4 | 1.0 | 1b | | | | 1 | | Dicot | Perennial forb | | |
| <i>Galium hardhamiae</i> | Rubiaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 1b | | | | 1 | | Dicot | Perennial forb | | |
| <i>Galium serpenticum</i> ssp. <i>scotticum</i> | Rubiaceae | SE | 5.9 | 29.5 | 5 | 6.0 | 0.4 | 0.2 | 1b | 1 | | | | | Dicot | Perennial forb | | |
| <i>Salix breweri</i> | Salicaceae | SE | 6.0 | 30 | 5 | 6.0 | 0.0 | 0.0 | | | 1 | 1 | 1 | | Dicot | Shrub | | |
| <i>Salix delnortensis</i> | Salicaceae | SE | 6.2 | 18.5 | 3 | 6.0 | 0.0 | 0.0 | 4 | 1 | | | | | Dicot | Shrub | | |
| <i>Salix stichensis</i> | Salicaceae | WI | 1.6 | 4.75 | 3 | 1.0 | 1.2 | 0.7 | | 1 | 1 | 1 | 1 | | Dicot | Tree, shrub | | |
| <i>Darlingtonia californica</i> | Sarraceniaceae | BE/SI | 4.1 | 32.5 | 8 | 4.0 | 1.4 | 0.5 | 4 | 1 | | | | 1 | Dicot | Perennial forb (carn.) | | |
| <i>Parnassia californica</i> | Saxifragaceae | WI | 2.0 | 6 | 3 | 2.0 | 0.0 | 0.0 | | 1 | 1 | | 1 | 1 | Dicot | Perennial forb | | |
| <i>Saxifraga howellii</i> | Saxifragaceae | BE/SI | 3.8 | 7.5 | 2 | 3.5 | 2.1 | 1.5 | 4 | 1 | | | | | Dicot | Perennial forb | | |
| <i>Antirrhinum cornutum</i> | Scrophulariaceae | WI | 2.2 | 11 | 5 | 2.0 | 0.8 | 0.4 | | | 1 | | | | Dicot | Annual forb | | |
| <i>Antirrhinum leptaleum</i> | Scrophulariaceae | WI | 1.6 | 3.1 | 2 | 1.6 | 2.1 | 1.5 | | | | | | 1 | Dicot | Annual forb | | |

APPENDIX 1. CONTINUED.

| Taxon ¹ | Family | Aff ² | Mean ³ | Sum ⁴ | Sources | Med. ⁵ | SD ⁶ | SE ⁷ | Rarity ⁸ | Geog. Dist. ⁹ | | | | | | Tax. Cat. ¹⁰ | Lifeform ¹¹ |
|---|------------------|------------------|-------------------|------------------|---------|-------------------|-----------------|-----------------|---------------------|--------------------------|----|----|----|----|--|-------------------------|---------------------------|
| | | | | | | | | | | KL | NC | BA | SC | SN | | | |
| <i>Minimus nudatus</i> | Scrophulariaceae | SE | 5.6 | 33.5 | 6 | 6.0 | 1.2 | 0.5 | 4 | | 1 | | | | | Dicot | Annual forb |
| <i>Minimus primuloides</i> ssp. <i>linearifolius</i> | Scrophulariaceae | BE/SI | 4.0 | 16 | 4 | 4.5 | 2.4 | 1.2 | | 1 | | | | | | Dicot | Perennial forb (rhiz.) |
| <i>Orthocarpus pachystachyus</i> | Scrophulariaceae | SE | 6.0 | 18 | 3 | 6.0 | 0.0 | 0.0 | | 1 | | | | | | Dicot | Annual forb (hemipar.) |
| <i>Pedicularis howellii</i> | Scrophulariaceae | SI | 2.5 | 7.5 | 3 | 3.0 | 1.2 | 0.7 | 4 | 1 | | | | | | Dicot | Perennial forb (hemipar.) |
| <i>Penstemon azureus</i> var. <i>azureus</i> | Scrophulariaceae | SI | 2.7 | 8 | 3 | 3.0 | 0.6 | 0.3 | | 1 | 1 | | | 1 | | Dicot | Perennial forb |
| <i>Penstemon filiformis</i> | Scrophulariaceae | BE | 3.0 | 30 | 6 | 5.5 | 1.3 | 0.5 | | 1 | | | | | | Dicot | Perennial forb |
| <i>Penstemon parvulus</i> | Scrophulariaceae | BE/SI | 3.7 | 11 | 3 | 4.0 | 0.6 | 0.3 | | 1 | | | | 1 | | Dicot | Perennial forb |
| <i>Penstemon purpusii</i> | Scrophulariaceae | SI | 2.8 | 11 | 4 | 2.0 | 2.4 | 1.2 | | 1 | 1 | | | | | Dicot | Perennial forb |
| <i>Triphysaria floribunda</i> | Scrophulariaceae | WI | 2.3 | 6.75 | 3 | 2.0 | 1.9 | 1.1 | 1b | 1 | 1 | 1 | 1 | | | Dicot | Annual forb |
| <i>Veronica copelandii</i> | Scrophulariaceae | SE | 6.1 | 24.5 | 4 | 6.0 | 0.0 | 0.0 | 4 | 1 | | | | | | Dicot | Perennial forb |
| <i>Fremontodendron californicum</i> ssp. <i>decumbens</i> | Sterculiaceae | BE/SI | 2.0 | 8 | 4 | 1.5 | 2.4 | 1.2 | 1b | | | | | 1 | | Dicot | Shrub |
| <i>Verbena californica</i> | Verbenaceae | BE | 4.8 | 14.5 | 3 | 4.0 | 1.2 | 0.7 | 1b | | | | | 1 | | Dicot | Perennial forb |
| <i>Viola cuneata</i> | Violaceae | BE | 5.2 | 31 | 6 | 6.0 | 1.3 | 0.5 | | 1 | 1 | | | | | Dicot | Perennial forb |
| <i>Viola douglasii</i> | Violaceae | SI | 2.8 | 13.75 | 5 | 2.0 | 2.0 | 0.9 | | 1 | 1 | 1 | 1 | | | Dicot | Perennial forb |
| <i>Viola hallii</i> | Violaceae | BE/SI | 4.0 | 16 | 4 | 4.0 | 2.3 | 1.2 | | 1 | 1 | | | | | Dicot | Perennial forb |
| <i>Viola lobata</i> ssp. <i>lobata</i> | Violaceae | WI | 2.3 | 11.35 | 5 | 2.0 | 2.4 | 1.1 | | 1 | 1 | | | 1 | | Dicot | Perennial forb (rhiz.) |
| <i>Viola ocellata</i> | Violaceae | SI | 2.5 | 12.5 | 5 | 3.0 | 0.9 | 0.4 | | 1 | 1 | 1 | 1 | | | Dicot | Perennial forb |
| <i>Viola primulifolia</i> ssp. <i>occidentalis</i> | Violaceae | BE | 5.1 | 25.5 | 5 | 6.0 | 1.4 | 0.6 | 1b | 1 | | | | | | Dicot | Perennial forb (rhiz.) |
| <i>Viola purpurea</i> ssp. <i>integrifolia</i> | Violaceae | WI/IN | 1.3 | 4 | 3 | 2.0 | 1.2 | 0.7 | | 1 | 1 | | | 1 | | Dicot | Perennial forb |

PSOROTHAMNUS FREMONTII AND *PSOROTHAMNUS ARBORESCENS*
(FABACEAE) IN CALIFORNIA

JAMES D. ADAMS, JR.

USC School of Pharmacy, 1985 Zonal Ave, Los Angeles, CA 90089-9121
jadams@usc.edu

DANA A. YORK

Umpqua National Forest Supervisor's Office, NW Stewart Parkway,
Roseburg, OR 97470
dayork@fs.fed.us

ABSTRACT

This note addresses the identification and California distribution of *Psorothamnus fremontii* (A. Gray) Barneby s.l. and *P. arborescens* (A. Gray) Barneby s.l. Both plants are generically known as indigo bush. *Psorothamnus fremontii*, sometimes called Fremont's indigo bush, can only be distinguished from *P. arborescens* by analysis of the seed pods, which differ in size, arrangement and exudates of their glands. The distribution of *P. fremontii* is very limited in California, restricted to the Grapevine Mountains, in Death Valley National Park, near the Nevada border, and the Providence Mountains, California State Recreation Area and nearby Lavic. *Psorothamnus arborescens* is much more common in California and occurs throughout the Mojave Desert and barely into the Great Basin Desert, from near Mount San Jacinto to the White Mountains.

Key Words: *Psorothamnus fremontii*, *Psorothamnus arborescens*, California, identification, locations.

We became interested in locating *Psorothamnus fremontii* because it may have been used medicinally (Garcia and Adams 2005). After searching the desert, reading articles written about the plant, talking to botanists, searching herbaria, publications and on-line resources, we began to wonder if *Psorothamnus fremontii* actually occurs in California.

Psorothamnus arborescens (A. Gray) Barneby and *P. fremontii* (A. Gray) Barneby were initially collected by John Fremont on his second expedition into California (Smucker and Fremont 1856). On April 25, 1844, he recorded in his journal the discovery of a new psoralea, "handsome leguminous shrub, three or four feet high, with fine bright purple flowers." When he made the discovery he was probably in the Silurian Valley, California, about 25 mi southwest of Bitter Spring at 35°13'08"N, 116°23'28"W, as measured by Fremont. However, Fremont did not publish the plant description himself. Fremont sent his specimens to the botanist John Torrey, who wrote a description of the plant in latin. This description was sent to another botanist, Asa Gray who included it in an article he wrote (Gray 1855). In this article, Asa Gray reported that Fremont had collected *Dalea arborescens* somewhere east of the Sierra Nevada Mountains. A translation of Torrey's technical description is presented below.

"*Dalea arborescens* (Torr. ined.) many branches, with glands, subspinous, adult branches glabrous, young branches, leaves and calyxes tomentose, the leaves are opposite, uneven and obovate, the inflorescence is in short dense ears (like corn), sewn

together by small bracts, calyx with sharp teeth, the bell shaped flower tube is the same length as the calyx, the two (lobes) above are oblong-triangular, the other (lobes) are narrow lanceolate and purple."

A further description was provided by Asa Gray, who wrote that "*D. arborescens* is a small tree, with few glands. A few minute, tubercular glands are found on the branches after removing the woolly covering. The leaves are petioled. The flower calyxes are large."

Asa Gray wrote that *P. fremontii* was collected and described by Fremont during the month of May, 1844, somewhere west of the Colorado River (Gray 1855). In May, Fremont was in Nevada (Smucker and Fremont 1856). He marched across southern Nevada to the Virgin River gorge. Nowhere in Fremont's diary does he record the collection of *P. fremontii*. This was entirely left for Torrey to describe and Gray to report. The description from Torrey, published by Gray, was in latin and is translated below.

"*Dalea fremontii* (Torr. ined.) bushy, many branches, few punctate glands, silken hairs, petiolate leaves (leaflets?), simple obovate-spatulate, trifoliate leaves in even multiples, leaves obovate, subspinescent twigs, inflorescence wide, sessile, open, crowded spikes, bracts often awl shaped and crowded, bell shaped tube, two (lobes) above are triangular, the rest are awl shaped, corolla purple, obcordate flag and keel are thick."

Torrey did not describe the seed pods of either *P. arborescens* or *P. fremontii*. Asa Gray did not add anything about the seed pods. He did write ad-

ditional information about *P. fremontii*. "It has copious reddish purple flowers. The calyx is minutely silky pubescent. The young parts of the plant have many inconspicuous glands. The leaflets are shorter than the petioles." It is not clear how Gray separated the species *D. arborescens* and *D. fremontii*. His description hints at the presence of more glands on the young branches of *fremontii* than *arborescens*. This is an observation we disagree with.

Barneby wrote extensively about *Psorothamnus* and was responsible for placing *P. arborescens* and *P. fremontii* in *Psorothamnus* rather than *Dalea* (Barneby 1977). *Dalea* plants are usually unarmed, whereas *Psorothamnus* generally have thorns or at least sharply pointed twigs. The calyx tube in *Dalea* is 10-ribbed, whereas *Psorothamnus* simply has unequal calyx lobes. There are 10 stamens in *Psorothamnus*, but 5, 9 or 10 stamens in *Dalea*. Barneby wrote that the geographic distribution of the plants is usually the key to identifying the species or subspecies (Barneby 1977). He did, however, note that *P. arborescens* and *P. fremontii* are "... sharply characterized by the pods. The seed pods of *P. fremontii* were covered with orange glands that run together forming lines or ridges. The seed pods of *P. arborescens* had a few, large, blister like glands scattered in a polka dot pattern." The surface of the *P. fremontii* pods was described as caramelized. Barneby described four subspecies of *P. arborescens*, mostly based on geographic distribution as, *simplifolius*, *arborescens*, *pubescens* and *minutifolius*. *Psorothamnus fremontii*, he claimed, is found only in the far eastern Mohave Desert. He defined two subspecies, again largely based on geographic distribution, *fremontii* and *attenuatus*.

Isely (1998) also found that *P. arborescens* and *P. fremontii* could be distinguished based on the glands found on the seed pods. The pods of *P. arborescens* had large glands randomly distributed. *Psorothamnus fremontii* had numerous small glands that tended to merge forming ridges. Isely recognized four subspecies of *P. arborescens* and two subspecies of *P. fremontii* based almost entirely on geographic distribution, just as Barneby had done earlier. The Jepson manual section on *Psorothamnus* was written by Isely and requires seed pods to identify the species, *fremontii* and *arborescens* (Hickman 1993).

The senior author visited the herbaria at Rancho Santa Ana Botanical Gardens, Claremont, California (RSA), the University of California Berkeley (JEPS) and the California Academy of Sciences, San Francisco (CAS) to examine specimens of *P. fremontii* and *P. arborescens*. Many of the *P. fremontii* specimens lacked seed pods and appeared to have been identified based on geography. The senior author examined 20 specimens labeled *P. arborescens* and 10 specimens labeled *P. fremontii* in Claremont. None of the *P. fremontii* specimens contained seed pods. Positive identification of the specimens was therefore not possible. Most of the

specimens had been previously identified by others, apparently based on geographic distribution. Some of the *P. arborescens* specimens had seed pods. The sparse glands on these seed pods were large and randomly arranged.

At the University of California, Berkeley, about 40 specimens were examined. None of the specimens labeled *P. fremontii* from California had seed pods. These could not be positively identified. Three of the Nevada *P. fremontii* specimens had seed pods. The glands were red-brown on all seed pods from the three plants. One plant came from the bajada west of Sand Canyon in the Pintwater Range near Indian Springs Valley, Nevada collected June 3, 1979. This plant had one seed pod that had many small glands with red-brown exudates that sometimes fused forming lines at the tip or the ventral portion of the seed pods (Fig. 1A). Other seed pods from this plant had small glands with small spots of exudates that tended to occur in rows. The glands were larger at the tip and the ventral part of the seed pods. Another specimen was collected from Charleston Park in the Charleston Mountains, Clark Co, Nevada on May 28, 1939. The glands on the seed pods were small with small spots of red-brown exudates and tended to occur in rows (Fig. 1B). There was no merging of glands to form lines in this specimen. Some of the *P. fremontii* seed pods had hairs regularly distributed across the pod surface. Other seed pods had hairs mostly on the dorsal part, but not on the main body of the seed pod. All the examined *P. arborescens* seed pods had just a few large glands arbitrarily distributed on the seed pod (Fig. 1C). Some of the seed pods had hairs on the dorsal edges. Plants seen in the wild had seed pods very similar to the one shown (Fig. 1C).

At the California Academy of Sciences, about 40 specimens labeled *Psorothamnus fremontii* were examined. Specimens from Utah, Nevada and Arizona had numerous small glands on the seed pods that produced clear or red-brown exudate. These exudates tended to merge and caramelize the surface of the seed pods. In addition, there were two specimens from California that had seed pods with numerous small glands that produced abundant red-brown exudate. These California specimens were from the Providence Mountains, just 3.5 mi from Kelso, and from the Lavic area that is a few miles west of the Providence Mountains (Fig. 1E, F).

Narrow- or linear-leaved *Psorothamnus* specimens, have been described from the Whipple Mountains of California (Hickman 1993). These plants have leaves that are 1 mm or less wide and have been described as *P. fremontii* var. *attenuatus*. The very narrow leaves of these plants are a distinguishing characteristic, that set them apart from *P. arborescens*. The authors have not seen these plants or seed pods from these plants. The identification of these plants will have to wait until seed pods are eventually found.

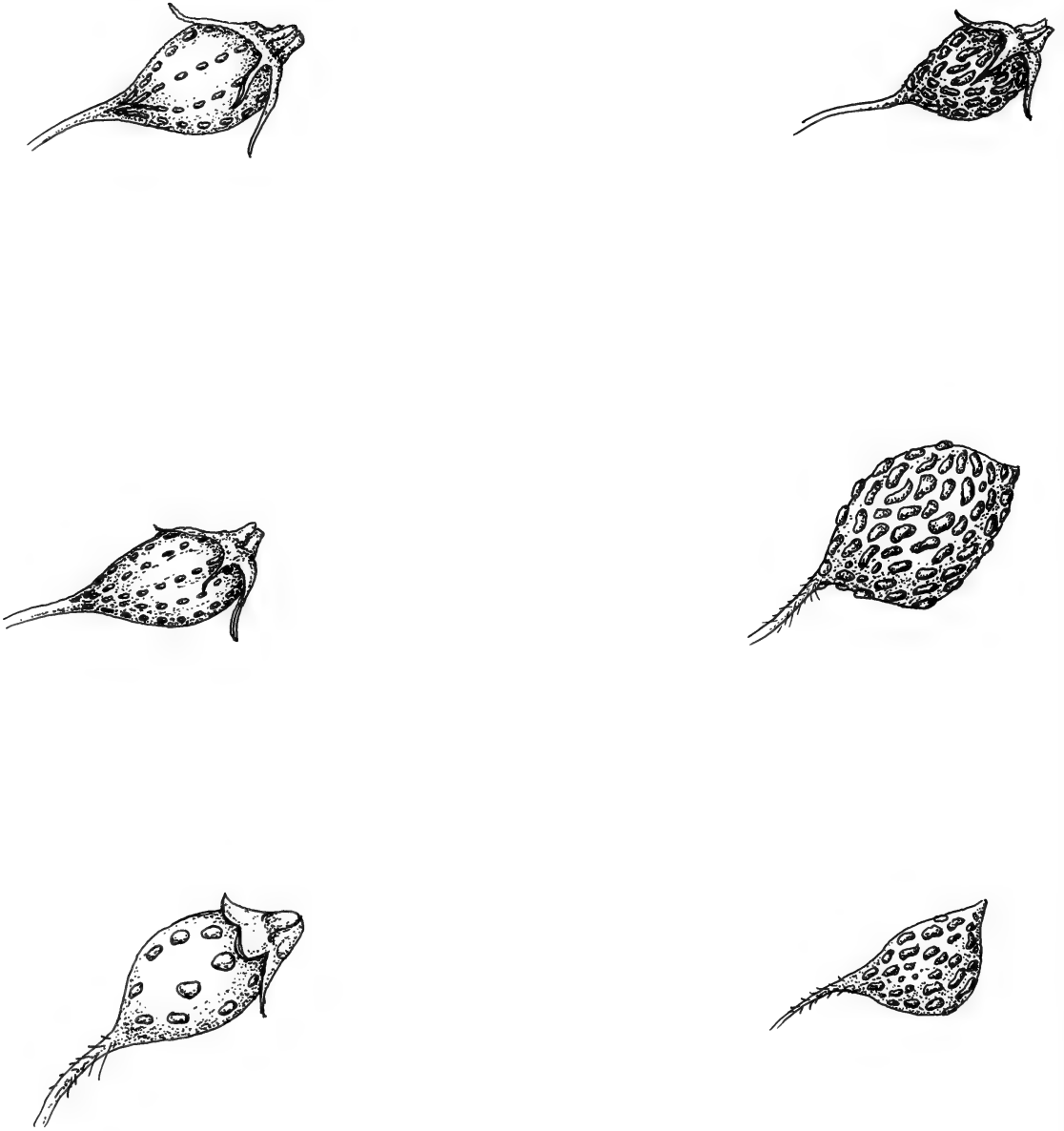


FIG. 1. Seed pods of *Psorothamnus fremontii* and *Psorothamnus arborescens*. From left to right, top to bottom, drawings are A, D; B, E; C, F. A *Psorothamnus fremontii* seed pod showing merged glands forming ridges, from a University of California Berkeley herbarium specimen at a Bajada west of Sand Canyon in the Pintwater Range, Indian Springs Valley, NV, June 3, 1979. B. *Psorothamnus fremontii* seed pod showing rows of glands, from a University of California Berkeley herbarium specimen collected in Charleston Park, Charleston Mountain, Clark County, NV, May 28, 1939. C. *Psorothamnus arborescens* seed pod showing large, scattered glands, from a University of California Berkeley herbarium specimen collected in Palm Springs, CA, December 18, 1938. D. *Psorothamnus fremontii* seed pod from Daylight Pass, Death Valley, CA, collected by the senior author on June 14, 2004. E. *Psorothamnus fremontii* seed pod from a herbarium specimen collected in the Providence Mountains, CA, 3.5 mi east of Kelso near Cornfield Springs. F. *Psorothamnus fremontii* seed pod from a California Academy of Sciences herbarium specimen found near Lavic, CA, May 20, 1920. Drawings are by Robert S. Amaral.

We have traveled extensively in the Mojave Desert of California looking for *Psorothamnus* specimens. *Psorothamnus arborescens* s.l. distribution in California extends south from Mono County to near Mt. San Jacinto. A geographically distinct popula-

tion has been reported in Northern Mexico (Isely 1998). We have found that *Psorothamnus arborescens* (A. Gray) Barneby var. *minutifolius* (Parish) Barneby occurs throughout Death Valley National Park, the White Mountains, and the Red Rock Can-

yon area. Specimens from Death Valley were collected and placed in the herbarium in the Death Valley National Park by the junior author. Identification was based on the appearance of large arbitrarily scattered glands on the seed pods. *Psorothamnus fremontii* var. *fremontii* was found only in the Grapevine Mountains along the California-Nevada border (Fig. 1D). Specimens were collected from the Grapevine Mountains, by both authors, and were placed in the herbarium at the Rancho Santa Ana Botanic Gardens, Claremont. California populations of *P. fremontii* were only previously reported to occur in San Bernardino County. The Grapevine Mountains plants had seed pods with no visible glands since the seed pods were covered with clear exudates. The exudates entirely covered the surfaces of the seed pods. The exudates were sticky enough to hold small rocks and plant material onto the seed pods. The exudates appeared to turn red-brown over time, giving the seed pods a caramelized appearance. We suggest that *P. fremontii* seed pods mature in May and June, and tend to mature after most flowers have withered on the plant. *Psorothamnus fremontii* may form only a few seed pods (20–50) on the entire plant. *Psorothamnus arborescens* seed pods mature in April and perhaps early May. The seed pods mature on the bottom of the raceme while flowers are still blooming on the top of the raceme. *Psorothamnus arborescens* may form many seed pods (more than 100) on each plant. The authors have not found both species growing together in any one area. We suggest that a more extensive investigation of the distribution of these two species should be based on seed pod characters and genetic analyses.

ACKNOWLEDGMENTS

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GROUP SELECTION EDGE EFFECTS ON THE VASCULAR PLANT COMMUNITY OF A SIERRA NEVADA OLD-GROWTH FOREST

ZACHARY E. KAYLER¹, LUCAS B. FORTIN² AND JOHN J. BATTLES
Department of Environmental Science, Policy and Management,
University of California, Berkeley, CA 94720

ABSTRACT

For an old-growth forest edge in the Sierra Nevada, we quantified the extent of edge effects from a group selection harvest. Across transects from the interior of the old-growth forest through the group selection opening, we quantified changes in resource availability (light, soil moisture, and seedbed) and vegetation composition (cover, richness). We found a steep change in light availability and community composition from the intact old-growth to the group selection. Both parametric and non-parametric multivariate analyses indicated two distinct plant associations, old-growth and group selection, with little indication of an edge association. Understory plant species richness normalized to a total area sampled of 0.25 ha was significantly greater in the group selection (74 species) than in the old-growth (55 species). *Chimaphila umbellata* and *Carex brainerdii* were the most abundant species in the old-growth and group selection respectively. *Tragopogon dubius* was the most abundant of six exotic species found in the group selection while there were no nonnative species found in the old-growth forest.

Key Words: Edge effects, group selection, plant diversity, Sierra Nevada, Old-growth.

The competing demands for timber products and forest preservation require land managers to evaluate simultaneously production and conservation objectives (Lindenmayer and Franklin 2002). For the Sierra Nevada of California, group selection has been proposed as a silviculture system that may accommodate production and conservation objectives (e.g., Herger-Feinstein 1998; USDA Forest Service 2002; USDA Forest Service 2003), but there is little quantitative information on the efficacy of such a system.

Group selection involves the periodic harvest of small groups of trees, typically between 0.1 and 1 ha (McDonald and Abbot 1994). Over the long term, a shifting mosaic of small patches of trees develops across the landscape. These patches will inevitably create a relatively large fraction of edge environment (e.g., York et al. 2003). In the context of group selection silviculture, the edge refers to the boundary between the opening created by harvesting a group of trees and the matrix of intact forest. York et al. (2003) reported a substantial edge effect on tree growth in group selection harvests. Given the significant influence of edges on ecological processes, other impacts are likely. In this paper, we assess the width and extent of potential edge influences on understory vascular plants at a forest-to-group edge created by a group selection harvest.

STUDY SITE

We conducted our study in a mixed conifer forest at the Plumas National Forest. Data was collected from a single group selection harvest and an adjacent long-term plot, the Baker plot (39°55'16"N 121°02'21"W). The Baker plot is a 4.5 ha old-growth mixed conifer stand with no record of recent fire (Ansley and Battles 1998).

The 1-ha group was harvested in 1993 at the north end of the Baker Plot. All overstory trees were felled and the remaining slash was piled and burned. Before planting ponderosa pine, the group was broadcast-burned. The area immediately adjacent to the Baker plot (a buffer approximately 12 m wide) was logged but not burned or replanted. To check for similarity in structure between the old-growth and harvested area, we reconstructed stand basal area from stump diameters and taper equations (Wensel and Olson 1995). Our estimates of basal area in the group selection plots fell well within the observed range of variation for plots of this size in the old-growth stand (59–148 m² ha⁻¹, Ansley 1998).

SAMPLING DESIGN

In 2000, we established three parallel transects along the gradient from the intact forest into the group selection (Fig. 1). Each 100-m long transect consisted of six equally spaced circular 0.031 ha plots. We designated plots along the dripline of the forest canopy as edge plots (0 m). The old-growth plots on the transect were then located -40 m, -20 m away from the drip line, while the group selection plots were located +20 m, +40 m and +60 m into the group selection.

Each circular study plot consisted of four 10 m

¹ Corresponding author. Current address: Forest Science Department, 321 Richardson Hall, Oregon State University, Corvallis, OR 97331. Email: zachary.kayler@oregonstate.edu

² Current address: School of Forest Resources and Conservation, University of Florida, Gainesville, FL 32611-0760

Baker Plot (USFS special use permit) (4.7 ha)

Group Selection (1ha)

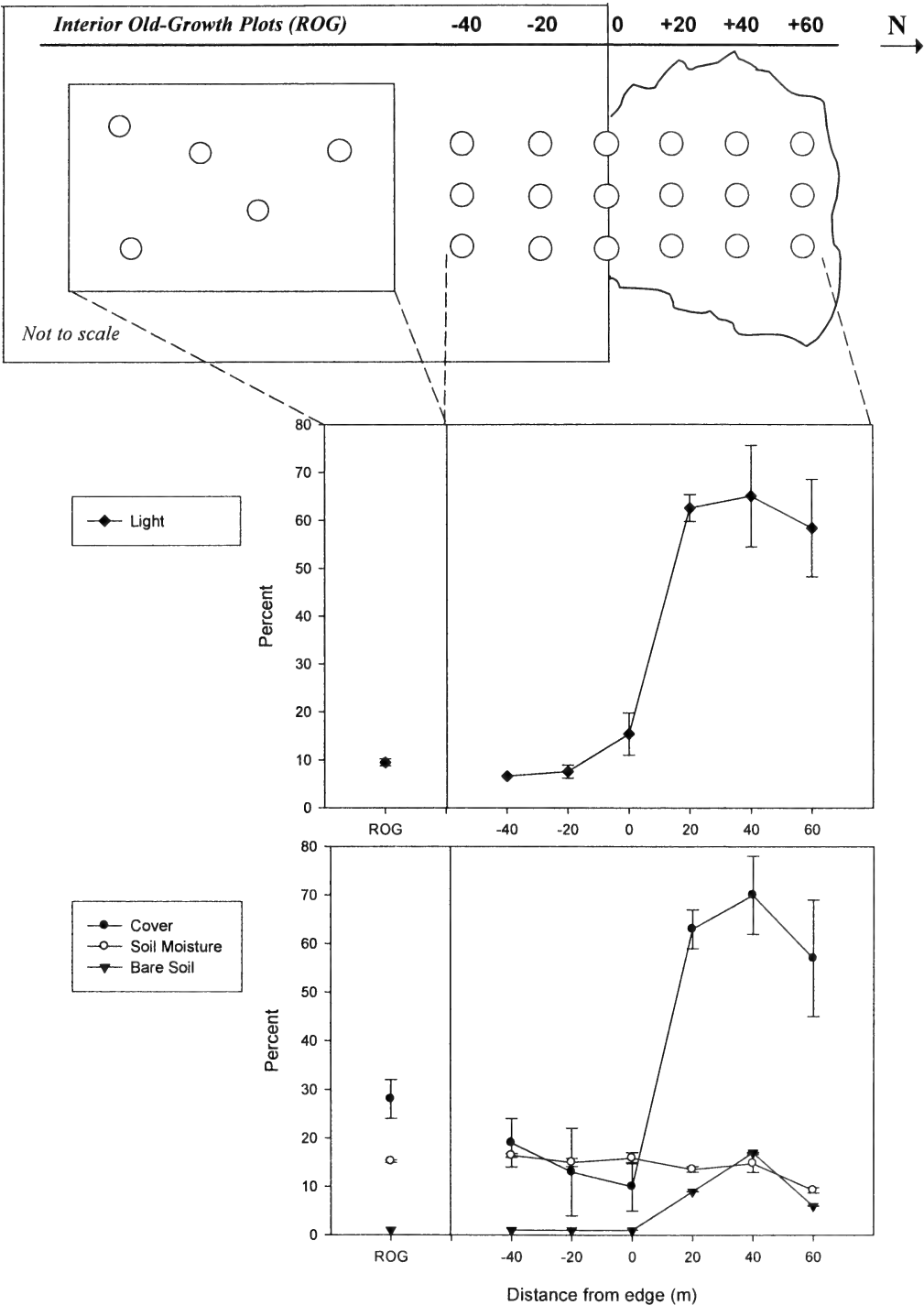


FIG. 1. (Top) Site layout at Baker old-growth forest, Plumas National Forest, California (Bottom) Mean and standard error of light availability at 1-m height (% TTR), understory plant cover measured by percent cover, soil moisture and bare soil for the 3 transects spanning the old-growth forest and group selection as well as the random old-growth plots (ROG).

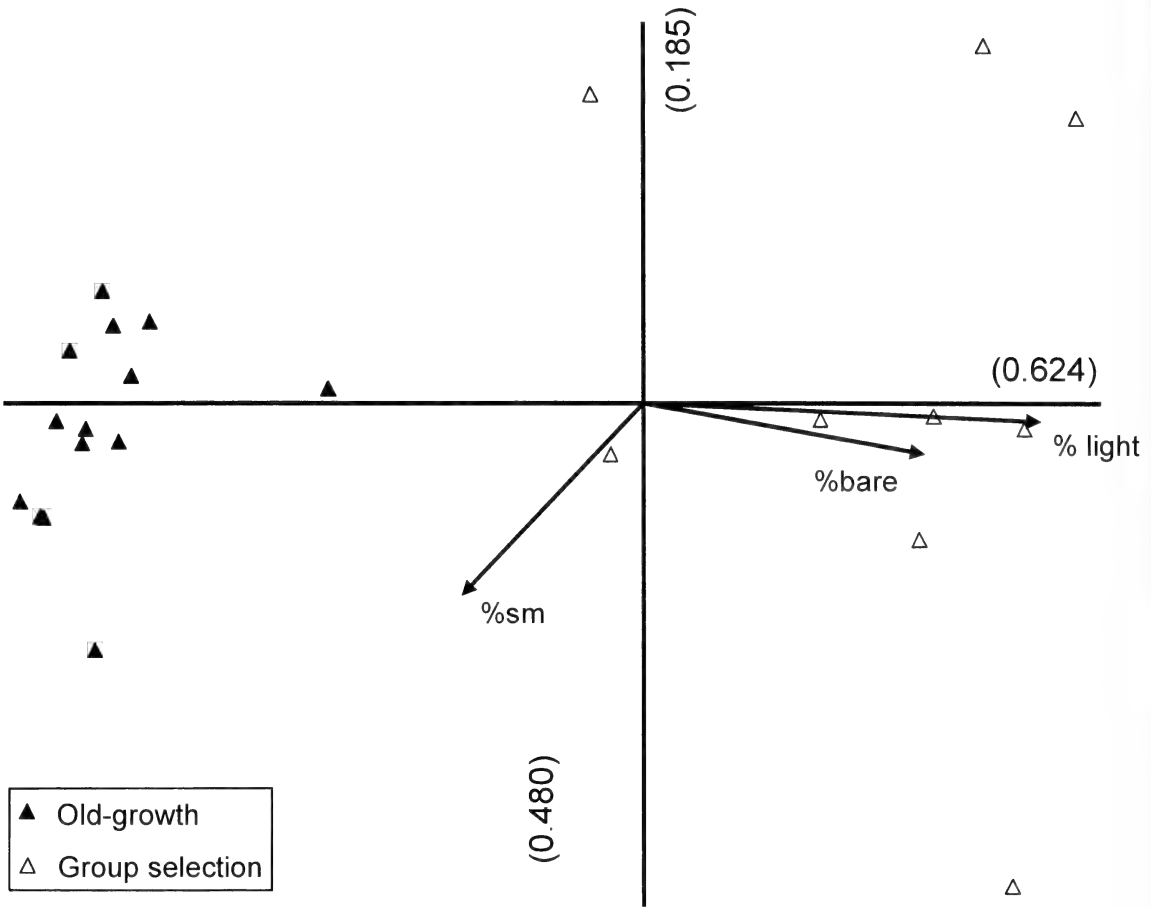


FIG. 2. CCA graph displaying the separation of plots by community according to vegetation and environmental data. Two distinct communities are shown, old-growth and group selection, with no ecotonal edge community in between. The community designation also reflects the TWINSpan groupings (open vs. closed triangles). CCA eigenvalues are in parenthesis along the axis. The correlation between species and specific environmental parameters are displayed graphically by the rays extending from the origin. The magnitude of the variables effect is depicted by the ray's length and the direction of plot placement by the angle. % sm = soil moisture, % bare = bare soil, % light = % TTR.

lines that radiated from the center along the cardinal directions. All quantitative environmental and botanical sampling was conducted along these lines. For each circular plot, two soil samples were taken at points 5 m north from plot center and 5 m south to a depth of 30 cm. Soil water content (g of water/100 g dry soil) was measured gravimetrically in June 2000. We used hemispherical photographs of the canopy to estimate light availability. Photographs were taken at plot center and points 7 m away from plot center in each cardinal direction at 1 m height. Photographs were analyzed using Gap Light Analyzer software (GLA http://www.rem.sfu.ca/forestry/downloads/gap_light_analyzer.htm) to calculate the percent of total transmitted radiation (%TTR), which estimates long-term average light levels.

We used line-point sampling to measure understory plant abundance and seedbed conditions in each plot. Every 10 cm we noted plant species (no-

menclature follows Hickman 1993) and classified the soil surface as fine litter, coarse woody debris or bare soil. Plot-level species richness was measured by conducting a timed census (two hr/plot).

We sampled random plots from the interior of the old-growth forest to check for differences with the transect plots at 20 m and 40 m into the old-growth. All interior plots were at least 60 m away from any edge—we refer to these plots as the random old-growth plots. Data collection in these plots followed the procedures described above.

We explored the relationship between the resource gradients and plant composition with canonical correspondence analysis (CCA). We used the CCA to ordinate plots in a state space defined by linear combinations of the environmental variables of light, soil moisture, and seedbed type (Palmer 1993). We used two-way indicator species analysis (TWINSpan), a divisive clustering program that classifies the plots based on species abundance (van

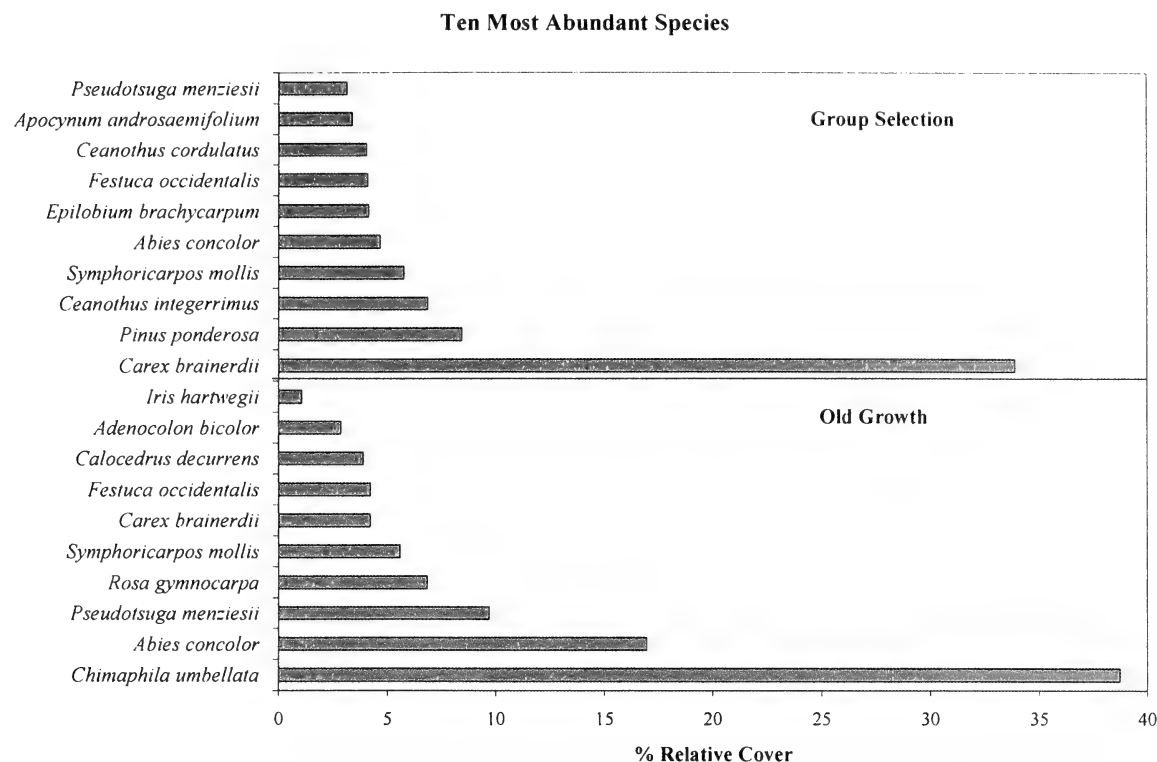


FIG. 3. Ten most abundant species by percent relative cover in each area: group selection and old-growth.

Tongeren 1995), as an independent measure of plot locations in ordination space. We used PC-ORD version 4 (MJM software, OR) to conduct all ordination and clustering analyses.

We relied on species richness as our primary measure of understory plant diversity. To account for the species-area relationship, we extrapolated species accumulation curves from sequential plot sampling (Colwell and Coddington 1994; Battles et al. 2001). Both species accumulation curves depict richness saturating at approximately nine sampled plots. Thus richness is reported as the mean of nine randomly resampled plots.

RESULTS

We observed a sharp and short gradient between old-growth and group selection plots (Fig. 1). While there was a slight increase in understory light on the edge relative to the nearest old-growth plots (-20), the difference between the edge and the nearest group plots ($+20$) was large. There were similar sharp increases at the edge in plant abundance as measured by cover and in the fraction of bare soil (Fig. 1).

The multivariate analyses also showed sharp differences between old-growth and group selection plots and did not detect an ecotone community that shares aspects of both communities. The CCA analysis produced two distinct clusters along the pri-

mary ordination gradient (Fig. 2). This primary axis is most correlated with understory light availability. The first division of the TWINSpan analysis (eigenvalue = 0.480) separated plots into the same groups as the CCA (Fig. 2) with no overlap between old-growth and group selection plots.

These results imply an edge effect on the understory plant community of less than 10 m in either direction. Moreover, we checked for bias in our comparison, in particular whether our plots into the old-growth were representative of the forest, by comparing the old-growth transect plots to the random plots from the interior of the Baker plot. In terms of key environmental metrics (i.e., light availability, seed bed, and soil moisture) and measures of the understory vegetation (i.e., composition, abundance, and species richness), we could detect no differences. At this site, edge effects were confined to a narrow area near the harvest boundary.

The lack of an ecotone is surprising given the differences between the adjacent plant associations. The group selection plots had significantly greater species richness. Based on a minimum sample of nine plots, mean species richness in the old-growth was 55 species (95% CI = 52–57 species). In the group selection, mean richness was 74 species (95% CI = 68–81 species). However, the understory vegetation was dominated by one species in each area (Fig. 3).

In the old-growth, *Chimaphila umbellata* was the most abundant species, while in the group selection *Carex brainerdii* dominated. *Chimaphila umbellata* is commonly found in early- and late-seral conifer forests (Halpern and Spies 1995) and small openings of managed forests with a well developed canopy (McDonald and Reynolds 1999). *Carex brainerdii* is often found in recently disturbed sites, dry forests and rocky soils (Hickman 1993). Overall, the old-growth association is characterized by late-seral, shade-tolerant species, five of which were unique to the old-growth. For example, *Chimaphila menziesii*, an uncommon species (Hickman 1993), *Goodyera oblongifolia*, and *Pyrola picta* were found exclusively in the old-growth, but at low abundance levels. Species found in the group selection that are associated with open and recently disturbed sites include *Ceanothus integerrimus*, *Epilobium angustifolium*, and *Apocynum androsaemifolium* (Hickman 1993). *Tragopogon dubius* was the most abundant of six nonnative species found in the group selection while in the old-growth we did not find any non-native species.

Given these differences between the two adjacent areas, the potential for an ecotone along the edge exists. Moreover, there were nonnative species established in the group selection that potentially could spread should the integrity of the surrounding forest canopy decline. As was clear from our results, the understory vegetation was sensitive to light availability. However, in this instance we did not observe edge effects on the understory plant community; although effects extending less than 10 m from the edge would not be observed due to our sample design. It is important to note that this study was at only one site and at one time. Site-specific attributes (e.g., the northern orientation of the forest edge) and different periods of post-harvest vegetation development may mask generalities. Therefore, research at additional sites is necessary to support generalizations regarding edge effects in the mixed conifer forests of the Sierra Nevada.

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PREPARATION AND QUANTIFICATION OF ENTOMOPHILOUS POLLEN USING SONICATION AND AN AREA-COUNTING TECHNIQUE

ALFRED KANNELY

Department of Biology, Yuba College, Marysville, CA 95901

Alfred@ofir.dk

ABSTRACT

Large pollen grains are difficult to quantify accurately. In order to ensure none have escaped, the anther must be removed and preserved before it is fully mature, leaving the pollen grains somewhat fragile and cohesive. Any method of quantification requires that they be separated into discrete grains, a difficult process, in part, due to their immature state. A probe sonicator can effectively disperse pollen grains from an opened anther in a petri dish partially filled with water. If the grains are too large to readily remain in suspension they can be allowed to settle in the petri dish and then quantified. As long as the grains are uniformly distributed in the petri dish, a compound microscope can be used to count the pollen grains in a field of view, and the contents of multiple fields of view can be used to extrapolate the total number of pollen grains.

Key Words: Sonication, pollen counting, entomophilous, *Calochortus*.

When studying reproductive biology, pollen counts are important because pollen/ovule ratio is an essential aspect of plant breeding systems (Crudden 1977). Methodology for the preparation and counting of entomophilous pollen grains from indehiscent anthers is complicated by several factors. In order to get accurate counts in terms of grains per anther, the sample anther must be indehiscent to ensure all pollen is present. Collecting young anthers often means the pollen grains are less developed, softer, and more fragile, thereby making complete grain removal from the anther more difficult. Furthermore, entomophilous pollen grains tend to be fairly sticky and may readily adhere to each other even once separated. Sonication, the process of passing sound waves through an aqueous medium, can be effective at separating pollen grains. Cohesion can be easily avoided with the addition of a surfactant (i.e., Triton X-100); however, the vibration produced by sonication causes excessive foaming, rendering the pollen difficult to view when a surfactant is added. Besides its cohesive properties, entomophilous pollen is difficult to count because it tends to be too large for a coulter counter and may be challenging to suspend in solution well enough to use a hemacytometer.

B. E. Vaissiere (1991, A. Dafni 1992) developed a protocol for pollen sonication using acetone as the solvent and a sonicator with a horn. However, this technique requires the sample to sit in acetone for thirty minutes prior to sonication. An alternative technique for sonication has been developed (Kannelly 2003). By using distilled water instead of acetone and a sonicator with a probe, the same results can be achieved in less time since the pollen does not need to sit in the water prior to sonication.

PROTOCOL FOR SONICATION OF POLLEN

Prepare the sample by placing a single indehiscent anther in a petri dish filled halfway with dis-

tilled water. The anther can either be fresh or preserved in a mixture of formalin, acetic acid and alcohol (FAA), a common botanical preservative. Then using forceps and a needle pull the anther sacs apart. Fix the sonicator's probe to a stationary stand and lift the petri dish until the probe is two thirds of the way to the bottom of the dish from the surface of the water. A model VC 50 Vibra Cell sonicator set at 20 μ m amplitude worked for a variety of *Calochortus* species (Liliaceae). The dish should then be moved around by hand to cause equal vibration throughout the entire area. The dish should also be raised and lowered slightly, which will cause the broken anther to move towards the probe and to break apart more. It is important to move the dish in straight lines, rather than in circles, as the latter will cause a current in the round dish that would prevent uniform settling of the pollen grains. Pieces of anther float in the suspension after sonication, and when lifted out with fine forceps and examined under a dissecting microscope, can be seen to be devoid of pollen.

Sonication between 12 and 15 seconds was adequate for most *Calochortus* species, depending on the maturity of the pollen grains. Maturity of pollen grains can be determined in the field by subjective comparisons between mature and immature filaments, anthers and pollen grains for a given species. Since most species ultimately reach different sizes it is best to sonicate anthers with a varying degree of maturity in order to find the optimal point. Less mature pollen grains can be mechanically damaged by sonication, but fully developed pollen grains spend a very short time in indehiscent anthers. The amount of time mature pollen grains will remain in indehiscent anthers varies according to species and weather conditions, as warm dry weather can increase the rate of flowering phenology.

After sonication, the pieces of anther remaining can be easily removed; as they will be floating on the water at the top since they have a low density. The empty anther can be removed with forceps and examined with a dissecting microscope to ensure all the pollen grains were removed. The petri dish should immediately be set where counting will be done so the pollen can settle in a single layer at the bottom of the dish.

COUNTING POLLEN (BY AREA)

Techniques for counting pollen vary in part based on grain size and number of grains produced per anther. Generally, entomophilous pollen is too large and heavy to count suspended in solution (with a hemacytometer or a coulter counter), and too numerous to count all individual grains. Jokerst (1980) counted pollen grains in a variety of *Calochortus* species with a hemacytometer. However, I found that *Calochortus* grains were too heavy in suspension and fell disproportionately in the channels of the hemacytometer. Kearns and Inouye (1993) describe a variety of general techniques for quantifying pollen. They only briefly mention using a microscope to scan a field of view. However, entomophilous pollen that has settled out of solution uniformly can be quantified by counting the number of pollen grains in a specified area. Ideally, the best technique would be to take a picture of all the pollen grains in the entire petri dish and quantify them using a computer program. Otherwise, a small subset of the total pollen, such as four fields of view at medium power (about 100 \times) under a compound microscope, can be counted and used to find the total number of pollen grains in the sample. Most entomophilous pollen grains settle to the bottom of a petri dish half filled with water in a matter of seconds whereas the rest of the particulate organic matter (remaining anther tissue) in the dish tends to float. Thus, it is possible to determine the number of pollen grains in the petri dish multiplying the number of pollen grains in the sample area by the fraction of the entire area of the dish (Fig. 1) that the sample area represents.

The field of view is the area viewed under medium power (100 \times) with a compound microscope; it is calculated after measuring the diameter with a stage micrometer. Then the diameter of the dish can be measured with calipers and its area calculated. A petri dish with walls perpendicular to the bottom must be used so area can be determined accurately. Care should be taken to use the same petri dish every time to ensure a consistent area measurement. For each sample (i.e., the contents of one anther), the number of pollen grains in four fields of view should be counted, one from each quadrant of the petri dish. Grains partially in view should be counted on the left half of the field of view and not counted on the right half. The totals can then be summed and used to determine the total number of

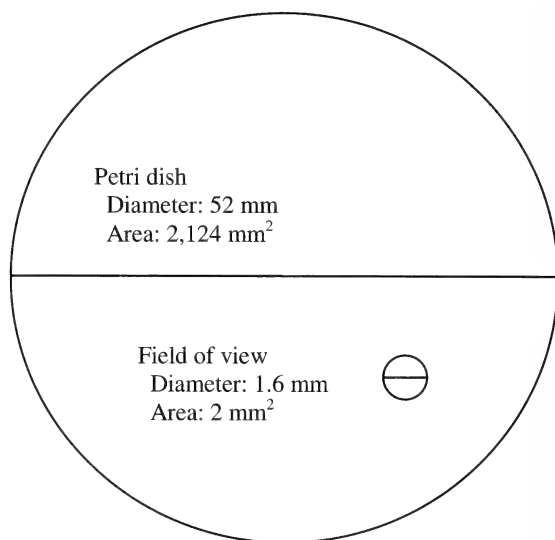


FIG. 1. Pollen Counting by Area (Πr^2), using petri dish and field of view diameters (not to scale).

pollen grains in the entire dish (i.e., in one anther). Each anther can be sampled, or one anther per flower can be used to determine the total number of pollen grains in the flower. Dish area and field of view area can be calculated as follows:

Pollen grains per dish =

$$\frac{(\text{total grains per fields of view counted})}{(\text{petri dish area})} \div \frac{(\text{total area of fields of view counted})}{1}$$

Pollen grains per flower =

$$(\text{grains per dish}) (\text{number of stamens})$$

ESTIMATION OF ACCURACY

Triteleia ixiodies ssp. *analina* (collected in Butte County, CA) was chosen to make total pollen counts because while it has entomophilous grains similar to *Calochortus* spp. it has a relatively low number of grains per anther (Schlising, unpublished). Total pollen grains per anther on three separate plants were counted with a dissecting microscope, resulting in counts of; 1620, 2228 and 1527, with an average of 1,792. In comparison, 24 plants of *T. ixoides* were sampled using the field of view estimation technique previously described. This count ($X \pm SE$) was 10 ± 0.8 per four fields counted, and the estimate for total grains per anther was 2158 ± 170 (range 1511–3670; $n = 24$).

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NOTEWORTHY COLLECTIONS

ARIZONA

ONCOSIPHON PILULIFERUM (L.f.) Källersjö [= *Colula pilulifera* L.f.; *Matricaria globifera* (Thunb.) Fenzl ex Harv.; *Pentzia globifera* (Thunb.) Hutch.; *Pentzia pilulifera* (L.f.) Fourc.] (ASTERACEAE).—Maricopa Co: Off Bartlett Dam Road, ca. 1.5 mi W of Bartlett Reservoir (east of the turn off to Horseshoe Lake), south side of road. On east-facing slope, in shallow soils. With *Parkinsonia microphylla*, *Opuntia engelmannii*, *Canotia holacantha*, *Yucca baccata*, *Simmondsia chinensis*, *Calliandra eriophylla*, *Cylindropuntia acanthocarpa*, 8 May 2003, Dixie Z. Damrel #V-898 (Tonto National Forest Herbarium, Phoenix). Pinal Co.: Casa Grande, hwy 84 ca. 0.1 mi W of Blanco, (32°52.771'N, 111°49.771'W), 1344 ft, roadside, May 2004, F. E. Northam 3 (ASU). Maricopa Co.: South side of West Lone Cactus Dr. at North Second Avenue, south of Deer Valley Airport (33°40'17"N, 112°4'40"W), 1000 ft., roadside with *Melilotus indicus*, *Sonchus asper*, *Lactuca serriola*, *Cynodon dactylon*, *Bromus*, *Ambrosia*, *Amsinckia intermedia*, *Sphaeralcea ambigua*, *Encelia farinosa*, 4 Mar 2005, J. Anderson 2005-11 (ASU). Maricopa Co: Phoenix, Pecos road S of South Mountain Park, W of 17th Ave (33°17'28"N, 112°6'29"W), large population along roadside in Sonoran Desert with much *Larrea tridentata*, ca. 1400 ft, 10 Apr 2004, L. R. Landrum & D. Lafferty 11010 (ASU). Maricopa Co: Phoenix, South Mountain Park (33°19'45.3"N, 112°2'30.7"W), upland desert over 0.5 mi from and road, with *Ambrosia dumosa*, *Encelia farinosa*, *Olneya tesota*, *Larrea tridentata*, *Parkinsonia microphylla*, 1600 ft, 24 Apr 2005, L. R. Landrum & D. Lafferty 11015 (ASU). Maricopa Co: On exit of I-17 and Happy Valley Road (33°42.607'N, 112°6.994'W), 1436', freeway exit roadside. Annual round golden heads, growing almost in a monoculture—abundant. 20 April 2005, Dixie Z. Damrel et al. 3084 (DES). Yavapai Co: Foothills of Black Mesa, near southern border of Agua Fria National Monument (34°5.147'N, 112°7.9701'W), 2055', Arizona Uplands Sonoran Desert Scrub with *Carnegiea gigantea*, *Parkinsonia microphylla*, *Eriastrum*, *Schismus*, *Echinocereus engelmannii*, *Celtis pallida*, *Larrea tridentata*, *Opuntia engelmannii*, *O. phaeacantha*, *Cylindropuntia acanthocarpa*, *Krameria erecta*, *Bromus rubens*, *Lotus salsuginosus brevixillus*, *L. strigosus tomentellus*, *Daucus pusillus*, *Plantago patagonica*, *Silene antirrhina*. Uncommon. 22 April 2005, Dixie Z. Damrel et al. 3102 (DES). Yavapai Co.: Agua Fria National Monument, floodplain of the Agua Fria River, east bank. South-central end of the AFNM (34°6.149'N, 112°6.142'W), 2114', loamy bottom soils of floodplain, disturbance-plant riparian. With *Hymenoclea salsola*, *Sisymbrium altissimum*, *Marah gilensis*, *Acacia greggii*, *Parkinsonia florida*, *Rumex hymenosepalus*, *Phalaris*, *Opuntia engelmannii*, *O. phaeacantha*, *Prosopis velutina*, *Bromus ssp.*, *Avena fatua*, *Malva parviflora*, *Hordeum murinum*, *Xanthium strumarium*, *Astragalus*. One small clump of two plants, both collected, 22 April 2005, Dixie Z. Damrel et al. 3117 (DES). Maricopa Co.: Inside Maricopa Flood Control area off of Jomax Rd., west of Cave Creek Rd. (33°44'28.5524"N, 112°02'47.70482"W), desert creosote flat with *Larrea tridentata*, *Ambrosia deltoidea*, *Lycium*, *Krameria grayi*, *Senna covesii*, *Cylindropuntia acanthocarpa*, *Echinocereus engelmannii*, *Ferocactus cylindraceus*, 499.72 m, 27 April 2005, Laura Dugan & Sean Whitcomb V91-7 (ASU). Maricopa Co.: Peoria, at a private residence on 95th Ave. (33°43'25.36680"N, 112°15'44.86971"W), residential area with construction underway, leading into desert with *Parkinsonia microphylla*, *Prosopis velutina*, *Larrea tridentata*, *Ambrosia deltoidea*, *Ziziphus obtusifolia*, *Senna artemisioides*, *Aloe*, 427.60 m, 27 April 2005. Laura Dugan & Sean Whitcomb Q91-9 (ASU). Maricopa Co.: State Trust Land SW of the intersection of I-17 and Hwy 74 (33°46'07.94954"N, 112°08'35.78422"W), desert creosote flat with *Larrea tridentata*, *Lycium*, *Cylindropuntia leptocaulis*, *C. acanthocarpa*, *Prosopis velutina*, 481.98 m, 06 April 2005. Laura Dugan & Sean Whitcomb T81-10 (ASU). Maricopa Co.: S of Skunk Creek, NW of the intersection of Joy Ranch Rd. and 19th Ave. (33°49'31.60311"N, 112°06'09.0270"W), desert creosote flat with small wash nearby with *Prosopis velutina*, *Cylindropuntia leptocaulis*, *C. acanthocarpa*, *Ambrosia deltoidea*, *Larrea tridentata*, *Sphaeralcea ambigua*, *Lycium*, *Ziziphus obtusifolia*, *Ferocactus cylindraceus*, 06 April 2005. Laura Dugan & Sean Whitcomb U61-10 (ASU). Maricopa Co.: E of 23rd Ave. and N of Dynamite Rd. (33°46'15.15084"N, 112°05'30.55646"W), at the juncture of desert creosote flat and upland foothills with *Larrea tridentata*, *Lycium*, *Krameria grayi*, *Ambrosia deltoidea*, *Senna covesii*, *Cylindropuntia acanthocarpa*, 493.47 m, 06 April 2005. Laura Dugan & Sean Whitcomb U81-17 (ASU). Maricopa Co.: 1.29 km E of the intersection of Lake Pleasant Rd. and Hwy 74 and 0.45 km N of Hwy 74 (33°48'07.84095"N, 112°13'43.43241"W), 479.32 m, desert with rocky soil, with *Cylindropuntia acanthocarpa* and weedy species, 12 May 2005, Laura Dugan & Sean Whitcomb R71-8 (ASU).

Previous knowledge. These are the first collections made of this species in Arizona as far as we know. It is already known in California (see A. C. Sanders, Madroño 43: 528. 1996; <http://ucjeps.berkeley.edu/cgi-bin/getcpn.pl?80983&expand=1>), the oldest known collection having been made in 1981. Photographs of Arizona plants have been posted on two websites, one [<http://www.home.earthlink.net/~chrstrask/OncPil01.pdf>] reporting a wild growing plant in 2003 at Seven Springs, a Forest Service Recreational site near Phoenix. This report is significant because a local botanical inventory was conducted there as recently as 2002, and *Oncosiphon* was not found (Doan 2002, Arizona State University, M.S. thesis).

Significance. *Oncosiphon piluliferum* is native to the Cape region of South Africa (Flora Capensis. Vol. 3, Harvey & Sonder. 1894). Common names include “stinkkruid” (Afrikaans), “stinknet” (Afrikaans), “cattle bush” and “globe chamomile” and the plant is indeed a relative of roman chamomile, *Chamaemelum nobile* (L.) All. The inflorescences are globe-like and the plant's odor is pungent. It is an attractive, graceful plant; seeds are offered for sale on the internet and it apparently has been sold in Arizona. We here list localities where single specimens were collected in 2003 and 2004 and 12 localities where the plant was collected during the spring of 2005. Such an apparently sudden appearance in the Phoenix area is probably real, as the plant seems to reproduce easily and to produce hundreds of small achenes. The spring of 2005

was especially wet and also coincided with a broad survey of the vegetation of the Phoenix area by the Central Arizona-Phoenix Long Term Ecological Research project at Arizona State University, making finding this plant more likely. In any case, as far as we know there are no prior collections in Arizona, but we expect *O. piluliferum* to become a widespread invasive species within a few years. We have observed additional populations along roads and in particular in natural desert conditions. The introduction of this species serves as an example of the potential impact of non-native ornamental plants, even attractive species, on native vegetation.

Prof A.E. van Wyk of the University of Pretoria in South Africa, was asked if he had any information about this species and he replied: "The widely used Afrikaans name "stinknet" means "stink only", because the plant is useless as a stock feed—it only stinks. Another commonly used local name, and perhaps the oldest in Afrikaans, is "stinkkruid", meaning "stink herb". In former times the plant was widely used medicinally in the Cape and it may have some virtues in this field. This is a strange species. Locally it has been reported from a very wide range of habitats and soil types, though usually in open, sunny locations. It behaves in a manner that makes one wonder whether it is really native to many parts of its current range in southern Africa. All over its range the species shows weedy tendencies by invading especially disturbed areas and cultivated fields. Being an annual, it is clearly a pioneer of disturbed sites. I suspect it is originally a species from the Cape Floristic Region, but due to agriculture has expanded locally beyond its original range. To confirm this one would have to trace the earliest known collections and check their localities. I can, however, confirm that it is not native to provinces such as North-West, Gauteng and Mpumalanga. Specimens from these areas are mainly from cultivated fields, especially fields that are under irrigation in winter. In such fields, the species can form dense, almost monospecific stands, whereas it is completely absent from adjacent natural vegetation. Hence in South Africa it clearly is a weed at times, a tendency which signals danger should the species spread far afield, as seems to be the case in the Phoenix area."

—L. R. LANDRUM, L. DUGAN, S. WHITCOMB, Arizona State University Herbarium, P.O. 874501, Tempe, AZ 85287. J. ANDERSON, BLM, Phoenix, AZ 85027. D. DAMREL, Desert Botanical Garden, Phoenix, AZ 85008. F. E. Northam, 216 E. Taylor St., Tempe, AZ 85281.

CALIFORNIA

DIGITARIA CALIFORNICA (Benth.) Henr. (POACEAE). San Diego County, 1 October 2003. Uncommon on rocky schist hillside at 33°03'N, 116°38'W, 290 m elevation, in Little Blair Valley, Anza-Borrego Desert State Park. Kim L. Marsden 154136 (SD), 1192 (BSA). [Det. by Larry Hendrickson, 2 October 2003].

Previous knowledge. Arizona cottontop is native to northern and central Mexico, Baja California, Mexico, and Colorado, Arizona, New Mexico and Texas in the southwestern U.S.. [Flora of North America 25 (part 2): 358–383; Hitchcock, A.S. (rev. A. Chase). 1971. Manual of the grasses of the U.S.. Dover Publications, Inc. New York.]

Significance. First report and collection for California. This collection extends the western range of this species from Baja California, Mexico, near 31°46'N, 116°01'W

[R. Moran, SD 63461] about 154 kilometers northward into southern California. The specific epithet *californica* refers to Baja California; the type collection is from Bahia Magdalena, Baja California, Mexico.

—KIM L. MARSDEN AND LARRY E. HENDRICKSON, California State Parks, Colorado Desert District, 200 Palm Canyon Drive, Borrego Springs, CA 92004.

DROSERA × *HYBRIDA* MACF. (DROSERACEAE)—Plumas county, California, 40°00.727'N, 120°59.586'W, elevation 1160 m, 1 September 2004. Plants were found flowering in a wet seep among *Drosera rotundifolia* L. at the Butterfly Valley Botanical Area near Quincy.

Previous knowledge. This taxon, a hybrid between the two eastern North American species *Drosera filiformis* Raf. and *Drosera intermedia* Hayne, is known only from a few locations in New Jersey (D.E. Schnell, 2002, Carnivorous Plants of the United States and Canada, Timber Press, Oregon, p 286); however, other populations of the hybrid may exist undetected in the eastern USA since the two parent species occur together in a number of other states (CT, MD, MA, NC, NY, RI for *Drosera filiformis* var. *filiformis*; AL, FL, GA, MS for *Drosera filiformis* var. *tracyi* (Macf. ex Diels) Diels). The colony of plants in Butterfly Valley, CA, was apparently introduced by carnivorous plant enthusiasts (in years past, other non-native carnivorous taxa have been found at this and other California sites).

Significance. This population of plants was detected by the author in September 2004. At that time, approximately 40–60 rosettes occupied an area only 20 × 40 cm in size. Although in flower, the inflorescences did not appear to be producing viable seed. (*Drosera* × *hybrida* is sterile.) Misidentifications of this cluster of plants are responsible for previous listings of *Drosera anglica* Huds. in Butterfly Valley, for example Forest Service records list the discovery of this cluster of plants, as "*Drosera anglica*," by botanists in 18–19 September, 1992 (Jim Belsher-Howe, Plumas Forest Service, private communication). While *Drosera anglica* can be found in several sites within 50 km of this location, no genuine populations have been found in the Butterfly Valley Botanical Area. The two taxa can easily be separated by the shape of the glandular leaf blade; the leaf blade of *Drosera anglica* is approximately (2.5)3–7(10) times longer than wide, while the leaf blade of *Drosera* × *hybrida* is approximately 45–65 times longer than wide.

Drosera × *hybrida* reproduces by vegetative means only, primarily by the annual production of a few lateral hibernacula each fall. As such, this plant has very little chance of being a significant conservation threat to the Butterfly Valley Botanical Area. However, if horticulturists continue to use the area as a dumping ground for non-native carnivorous plants, an intractable greenhouse weed such as *Utricularia subulata* will eventually be introduced (perhaps unintentionally), as has already occurred in the Mendocino County pygmy forests.

Permission to collect specimens of these plants was kindly granted by staff of the Plumas National Forest Service. Live specimens have been placed in the University of California, Davis, Conservatory, for further study; an herbarium specimen has been stored at the University of California, Davis (DAV), #BR040901.

—BARRY A. RICE, International Carnivorous Plant Society, P.O. Box 72741, Davis, CA 95617.

UTRICULARIA OCHROLEUCA HARTM. (LENTIBULARIACEAE)—El Dorado county, California, 38°47.719'N, 119°58.012'W, elevation 2350 m, 7 August 2004. Grass Lake, near Luther's Pass. Plants were found in sterile condition in a few cm of water on the floating vegetation mat.

Previous knowledge. Circumboreal, found in northern, central, and western Europe, Afghanistan, Japan, and North America. In North America, found in several Canadian provinces, south to the USA (Washington, Oregon, California, Colorado, Ohio, Illinois, Michigan, MN). It was first detected in California in 1994 at Lake Almanor in Plumas County (J.H. Rondeau, Madroño, 1998, 45: 184–185). In 1998 I detected it at a new site (Willow Lake, less than 15 km to the northwest). However, its first known herbarium collection in California (CHSC 54403) was actually in 1991 from yet another nearby site (Little Willow Lake) but this collection was misclassified as *U. intermedia* Hayne; in 2004 I examined this specimen and correctly identified it as *U. ochroleuca*. The new collection, at Grass Lake in El Dorado County, is approximately 210 km to the southeast of the three Plumas County locations.

Significance. This new location at Grass Lake represents a significant range extension south in California. Often confused with the more common *Utricularia intermedia* Hayne, *Utricularia ochroleuca* can be distinguished using gross vegetative characters (P. Taylor, *The Genus Utricularia: a Taxonomic Monograph*, 1989, Kew Bulletin Additional Series XIV). Goran Thor (*Nord. J. Bot.*, 1988, 8(3): 213–225.) emphasizes the use of bladder quadrifid glands to identify boreal *Utricularia* species, and uses quadrifid gland criteria to divide *Utricularia ochroleuca* sensu lato into a more narrowly defined *Utricularia ochroleuca* sensu stricto and *Utricularia stygia* Thor. Using his criteria, previous collections of *Utricularia ochroleuca* in Willow Lake and Little Willow Lake would be more properly interpreted as *Utricularia stygia*. If this interpretation is correct, the Willow Lake and Little Willow Lake plants would be the only stations for *Utricularia stygia* in the lower 48 states of the USA (E. Schlosser, *Carnivorous Plant Newsletter*, 2003, 32: 113–121). It is unclear if the Lake Almanor plants are more closely allied with *U. stygia* or *U. ochroleuca* s. str. In contrast, quadrifid gland arms in the plants from Grass Lake indicate these plants are *Utricularia ochroleuca* s. str. Previous records of *U. stygia* in North America are restricted to Canada (Nova Scotia, and Northwest Territories) and Alaska (Thor 1988).

The population of plants found at Grass Lake was small, so a relatively depauperate collection was obtained for the Herbarium (DAV) at the University of California, Davis, #BR040801.

The three species (*U. intermedia*, *U. stygia*, and *U. ochroleuca* s. str.) can be distinguished using the following vegetative features. Quadrifid gland observations must be made at 200× or higher magnification. Floral characters are not noted below since the latter two species rarely flower in California. The interested reader is encouraged to pursue further details in the works by Taylor, Thor, and Schlosser cited above.

Utricularia intermedia: Stolon shoots markedly dimorphic (the green surface shoots bear only finely dissected leaves, the descending shoots bear bladders only); ultimate leaf segments bear 5–12 setulose bristles on leaf margins; the four arms of the bladder quadrifid glands are in oppositely directed pairs of parallel arms (i.e., diverging by 0–30 degrees); leaf tips acute to obtuse.

Utricularia ochroleuca s. lat.: Stolon shoots weakly di-

morphic (all shoots bear both dissected leaves and bladders, but the relative proportions of leaves vs. bladders subject to variation); ultimate leaf segments bear 2–7 setulose bristles on pronounced marginal teeth; the four arms of the bladder quadrifid glands are in two oppositely directed pairs, where each pair of arms diverge by more than 30 degrees; leaf tips acute. In *Utricularia ochroleuca* s. str., the pair of long gland arms diverge by 30–45 degrees; the pair of short arms diverge by 90–160 degrees. In *Utricularia stygia*, the pair of long gland arms diverge by 20–45 degrees; the pair of short arms diverge by 40–80 degrees.

—BARRY A. RICE, International Carnivorous Plant Society, P.O. Box 72741, Davis, CA 95617.

SALVINIA MOLESTA D. S. Mitch. (SALVINIACEAE).—Orange Co., City of Anaheim, flood plain N of Santa Ana River, Anaheim Wetlands Reserve, ca. 0.5 km E of Wier Canyon Rd., uncommon but widespread in a large constructed pond overgrown with *Eichhornia crassipes* (Mart.) Solms., UTM 11S 430914E 3748784N (NAD 83) [33°52'38"N 117°44'49"W], elev. 102 m (334'), 25 Sep 2004, Riefner 04-441 (RSA).

Previous knowledge. *Salvinia molesta* (giant salvinia, Kariba weed) is an invasive, free-floating aquatic fern native to South America (Brazil), which has become a troublesome pest in Africa, Australia, Hawaii, India, Mauritius, New Guinea, Sri Lanka, New Zealand, and elsewhere (Holm et al. 1977, *The World's worst weeds: Distribution and biology*, University Press of Hawaii, Honolulu; Meyer 2000, in: Sherley [tech. ed.], *Invasive species in the Pacific*, South Pacific Regional Environment Programme, Samoa). In the U.S., *S. molesta* was first observed outside of cultivation in South Carolina (Johnson 1995, *Aquatics* 17:22). It has now also been reported in Alabama, Florida, Georgia, Louisiana, Mississippi, North Carolina, Texas, and as far west as Arizona and California (Jacono et al. 2001, *Castanea* 66:214–226; DiTomaso and Healy 2003, *Aquatic and Riparian Weeds of the West*, University of California Agriculture and Natural Resource Publication 3421, Oakland). Records in California are from canals in the lower Colorado River drainage near Winterhaven in Imperial County and near Blythe in Riverside County, and private ponds in San Diego (Fallbrook) and San Luis Obispo (Price Canyon Rd.) counties (Hrusa et al. 2002, Madroño 49:61–98). *Salvinia molesta* has also been reported from the San Diego River, San Diego County, but no specimen has been seen (Hrusa et al. *loc. cit.*). The Fallbrook pond population, also in San Diego County, may have been purposely planted for cultivation and sale (Hrusa et al. *loc. cit.*).

Significance. This collection represents the first record from Orange County and the Santa Ana River watershed, and the first confirmed naturalized occurrence of giant salvinia from coastal lowlands in southern California. *Salvinia molesta* is one of the world's worst aquatic pests (Holm et al. 1997, *World weeds: Natural histories and distribution*, John Wiley and Sons, NY). It is a federally listed noxious weed (Plant Protection and Quarantine 2002, Federal noxious weed list, USDA Animal and Plant Health Inspection Service, Washington, DC.) that has the potential to significantly affect the ecology of freshwater habitats throughout much of the southern U.S. (Federal Register 2003, Vol. 68:9633–9634). *Salvinia molesta* is also recognized as a species with the potential to spread explosively in California (CAL-EPPC 1999, in: Anderson

et al. [eds.], Exotic plants of greatest ecological concern in California, California Exotic Pest Plant Council). *Salvinia molesta* may be expected to naturalize wherever water hyacinth (*E. crassipes*) persists or in areas that experience frost but not the formation of ice on freshwaters (Whiteman and Room 1991, Aquatic Botany 40:27–35; DiTomaso and Healy *loc. cit.*). Accordingly, *S. molesta* has apparently naturalized and is spreading in the mild Mediterranean climate of the southern California coastal zone, and should be expected elsewhere. Additional occurrences should be sought in low-lying, slow-moving waters of ponds, reservoirs, and wetlands, especially in the San Diego area and the Los Angeles basin, throughout the southern and central California coastal counties.

—RICHARD E. RIEFNER, JR., 5 Timbre, Rancho Santa Margarita, CA 92688 and STEVE BOYD, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Avenue, Claremont, CA 91711.

TROPIDOCARPUM CAPPARIDEUM E. Greene (BRASSICACEAE).—Monterey Co.: Fort Hunter Liggett. Adjacent to Gabilan Rd, ca. 1.3 km SSE of intersection with San Miguelito Loop Rd, Gabilan Valley. Scattered in frequently burned, open, annual, disturbed grassland in large swale on Salinas clay-loam, with *Avena barbata*, *Centaurea solstitialis*, *Bromus hordeaceus*, *Lupinus nanus*, and *Erodium* sp., near 35.9238°N, 121.2400°W, elev. ca. 350 m., 19 Apr 2000, Meredith Osborne 16, with Louann Guzman, Daryl Witmore, and Laura Eliassen (CDA, MO, SBBG), det. Ihsan Al-Shebazz (MO). West of Gabilan Crk, ca. 0.4 km S of jct of Gabilan and San Miguelito Loop roads; near 35.92725°N, 121.24181°W, elev. ca. 380 m., 29 Apr 2001, D.H. Wilken 15876 with A. Hazebrook and T. Morosco (JEPS, MO, SBBG), det. Ihsan Al-Shebazz (MO).

Previous knowledge. Known from northwestern San Joaquin Valley near Mt. Diablo (Alameda, Contra Costa, and San Joaquin counties) in grasslands on low hills and valleys with alkaline soils (P. Munz, A California Flora, 1963; R. Rollins, The Cruciferae of continental North America, 1993). Also reported from Glenn, Monterey, and Santa Clara counties (D. Tibor, editor, CNPS Inventory, 6th edition, 2001), but believed extirpated at all previously known sites. A specimen from Fresno County (H. de Forest in 1930, RSA) provides no location. A collection from "Jolon Grade", Monterey County by C. Thurcan in 1920 (RSA) belongs to *T. gracile* Hook. (det. Steve Boyd, RSA).

Significance. First verified records from Monterey County, and first observations since 1957. Previously considered extinct (D. Tibor, editor, CNPS Inventory, 6th edition, 2001). In 2001, the Gabilan Valley population consisted of ca. 300 plants scattered widely within 20 acres. In 2002, this population was more closely surveyed and ca. 600 plants were observed over the same area. A second population at Fort Hunter Liggett was found near El Piojo Creek, Long Valley, ca. 1.3 mi NW of Sam Jones Rd, near 35.889°N, 121.1731°W, Elev. 350 m, 13 May 1999, A. Hazebrook and S. Weis s.n., where it occurred in a frequently burned grassland/oak savanna on moderately alkaline, slowly draining silty clay soil with *Bromus hordeaceus*, *Vulpia myuros*, *Erodium cicutarium*, *Lupinus bicolor*, and *Hemizonia lobbii*.

—MEREDITH A. OSBORNE* and ARTHUR W. HAZEBROOK, Research Associates, Center for Environmental Management of Military Lands, Colorado State University, under contract to Fort Hunter Liggett, CA 93928-7110.

OREGON

ACER RUBRUM L. (ACERACEAE).—Lane Co., 6 m tree adventive in dense stand of *Carex obnupta* L. H. Bailey, disturbed wet prairie remnant, W of Danebo Street, N of Amazon Creek, Eugene, elev. 120 m, 7 Oct 2004, P. F. Zika & E. R. Alverson 20377 (OSC, WTU).

Previous knowledge. Red maple is native to eastern North America, west to Manitoba. It is commonly planted as an ornamental west of the Cascades in Oregon and Washington.

Significance. First report for Oregon as an escape from cultivation.

CAREX TRIBULOIDES Wahlenb. var. *TRIBULOIDES* (CYPERACEAE).—Multnomah Co., silty bank on E shore of Sandy River delta, elev. 5 m, 26 Jul 2000, P. F. Zika 15116 (MICH, WTU); dupl. det. by A. A. Reznicek).

Previous knowledge. Blunt broomsedge is native to eastern North America, west to Nebraska. It is adventive on the lower Fraser River in British Columbia (Douglas and Ceska 2001, In: Douglas et al. (eds.), Illustrated Flora of British Columbia, Vol. 6. Monocotyledons (Acoraceae through Najadaceae), British Columbia Ministry of Environment, Lands and Parks, Ministry of Forests, Victoria, BC, p. 18–158).

Significance. First record for Oregon.

COTONEASTER MUCRONATUS Franch. (ROSACEAE).—Benton Co., adventive in mesic disturbed forest, E slope of Witham Hill, elev. 100 m, 28 Oct 2003, P. F. Zika 19264 (OSC, WTU; dupl. det. J. Fryer); same site, 15 May 2004, P. F. Zika 19584 (WTU).

Previous knowledge. Native to western China. Mucronate cotoneaster is an infrequent ornamental planting in western Oregon. It escapes from cultivation in England (Stace 1997, New Flora of the British Isles, 2nd ed., Cambridge University Press, Cambridge, U.K.).

Significance. First collection as a wild plant in Oregon.

COTONEASTER NITENS Rehder & E. H. Wilson (ROSACEAE).—Lane Co., thickets, S slope of Skinner Butte, Eugene, elev. 165 m, 7 Nov 2004, E. R. Alverson s.n. (OSC).

Previous knowledge. Few-flowered cotoneaster is native to western China. It is infrequently planted in gardens, and is locally escaped from cultivation in King Co., Washington (Zika 2002, Madroño 49: 195–197).

Significance. First record as a garden escape in Oregon.

COTONEASTER PANNOSUS Franch. (ROSACEAE).—Jackson Co., adventive on dry forested slope, Waterline Road, Ashland, elev. 700 m, 19 May 2004, P. F. Zika 19658 (OSC).

Previous knowledge. Native to southwestern China. Silverleaf cotoneaster is a occasional escape from cultivation on the coast of California. Prior reports of this species from Oregon were based on misidentifications.

Significance. First collection as a wild plant in Oregon.

HEDERA COLCHICA (K. Koch) K. Koch (ARALIACEAE).—Curry Co., locally common, climbing 5 m into *Picea sitchensis* (Bong.) Carrière, *Thuja plicata* Donn ex D. Don, dense thickets along Route 101, near Coos County line, elev. 30 m, 17 May 2004, P. F. Zika 19623 (OSC, WTU).

Previous knowledge. Persian ivy is native to the Cau-

* Current address: California Department of Fish and Game, 4949 Viewridge Avenue, San Diego, CA, 92123.

casus, and commonly planted as an ornamental ground cover west of the Cascades in Oregon and Washington.

Significance. First record as an escape from cultivation in Oregon.

HEDERA HIBERNICA (G. Kirchn.) Bean (ARALIACEAE).—Benton Co., S of Corvallis, 16 Nov 1959, D. W. Frost s.n. (GH, WTU); disturbed mesic forest, E slope of Witham Hill, Corvallis, elev. 100 m, 15 May 2004, P. F. Zika 19585 (WTU); Clackamas Co., forested slope, West Mount Scott, elev. 210 m, 12 Mar 2004, P. F. Zika 19276 (OSC, WTU); Clatsop Co., Camp Rilea, SW of Warrenton, elev. 12 m, 7 Mar 1998, S. Sundberg 4293 (OSC); thickets, near Lincoln Street, Astoria, elev. 35 m, 14 May 2004, P. F. Zika 19557 (WTU); Coos Co., dominant weed near slough, Coquille, elev. 25 m, 17 May 2004, P. F. Zika 19612 (WTU); common weed, Myrtle Point, elev. 30 m, 17 May 2004, P. F. Zika 19604 (OSC); Curry Co., Marina Heights Road, Brookings, elev. 95 m, 18 May 2004, P. F. Zika 19628 (OSC); Douglas Co., E bank of Umpqua River, Roseburg, elev. 130 m, 21 May 2004, P. F. Zika 19667 (OSC); N bank of North Umpqua River, near Route 99 and Del Rio Road, elev. 160 m, 17 May 2004, P. F. Zika 19601 (WTU); Jackson Co., riparian weed, Ashland Creek near dam, Ashland, elev. 400 m, 19 May 2004, P. F. Zika 19653 (WTU); Lane Co., Lake Creek, near Green Creek Road, Coast Range, elev. 76 m, 2 Nov 1995, R. Halse 5005 (OSC); Lane Co. at Benton Co. line, Washburne Wayside, Route 99W, elev. 100 m, 21 May 2004, P. F. Zika 19673 (WTU); Multnomah Co., frequent escape in E Portland near Albina, 5 Oct 1927, J. W. Thompson 3933 (WTU); common adventive, second growth forest, SE Ogden Street, Portland, elev. 110 m, 12 Mar 2004, P. F. Zika 19281 (WTU).

Previous knowledge. *Hedera hibernica* (syn. *H. helix* L. subsp. *hibernica* (G. Kirchn.) D. C. McClint.), Atlantic ivy, is native to Europe, and widely introduced as a groundcover west of the Cascades. It is an allotetraploid frequently confused with the diploid *H. helix*, English ivy. They can be distinguished morphologically by subtle differences in the leaves and pubescence (McAllister and Rutherford 1990, Watsonia 18: 7–15; Vargas et al. 1999, Plant Syst. Evol. 219: 165–179). Both are pests in natural areas, but we have observed that the latter is less common as a wild plant, matching the conclusions of Murai (1999, Understanding the invasion of Pacific Northwest forests by English ivy (*Hedera* spp., Araliaceae). Unpublished M. S. thesis, College of Forest Resources, University of Washington, Seattle).

Significance. First collections as garden escapes in Oregon.

LONICERA MAACKII (Rupr.) Maxim. (CAPRIFOLIACEAE).—Lane Co., riparian forest, W bank of Willamette River, E of Merry Lane, Eugene, elev. 120 m, 27 Aug 2004, P. F. Zika 20094 & E. R. Alverson (UC, WTU); flowering in blackberry thickets, swale N of Irving Road near Shirley Street, Eugene, elev. 120 m, 15 May 2004, P. F. Zika 19581 & E. R. Alverson (OSC); fruiting, same site, 7 Oct 2004, P. F. Zika 20407 & E. R. Alverson (OSC, WTU).

Previous knowledge. An ornamental native to Asia. Amur honeysuckle is commonly escaped from cultivation

in eastern and central North America, where it is a species of considerable management concern due to its invasive tendencies.

Significance. First collections as a wild plant in Oregon.

MALUS SIEBOLDII (Regel) Rehder (ROSACEAE).—Lane Co., white flowers, damp thickets, wet prairie remnant, near W Fork Willow Creek, The Nature Conservancy Willow Creek Natural Area, Eugene, elev. 120 m, 27 Apr 2003, P. F. Zika 18268 (NY); whitish-pink flowers, damp thickets, shrub-invaded wet prairie remnant, near E Fork Willow Creek, The Nature Conservancy Willow Creek Natural Area, Eugene, elev. 120 m, 27 Apr 2003, P. F. Zika 18273 (OSC, WTU); same site, red fruits, 27 Aug 2004, P. F. Zika 20111 (OSC); same site, yellow-brown fruits, 7 Oct 2004, P. F. Zika 20380 (WTU); red fruits, disturbed wet prairie remnant, W of Danebo Street, N of Amazon Creek, Eugene, elev. 120 m, 7 Oct 2004, P. F. Zika & E. R. Alverson 20375 (OSC, UC, WTU).

Previous knowledge. Native to China, Korea, and Japan. Toringo crabapple is a common ornamental species west of the Cascades in Oregon and Washington. Previously reported as *Malus floribunda* Siebold ex Van Houtte (Simpson et al. 2002, Vascular Plants of Lane County, Oregon, An Annotated Checklist, Emerald Chapter Native Plant Society of Oregon, Eugene, OR), a similar species that lacks strongly lobed leaves on vigorous shoots. *Malus sieboldii* has strongly lobed leaves on the most vigorous shoots, although these are not always evident on slow-growing plants until late in the season.

Significance. First report as an escape from cultivation in Oregon.

OXALIS DEBILIS Kunth var. *CORYMBOSA* (DC.) Lourteig (OXALIDACEAE).—Coos Co., lawn weed, Railroad Avenue, Myrtle Point, elev. 30 m, 17 May 2004, P. F. Zika 19602 (OSC); partly shaded slope, South Irving Street, Coquille, elev. 60 m, 17 May 2004, P. F. Zika 19620 (WTU); lawn weed, Third Street SE, Bandon, elev. 25 m, 17 May 2004, P. F. Zika 19622 (OSC, MO).

Previous knowledge. Large-flowered pink sorrel is native to South America, and weedy in the southeastern U.S. It is planted in gardens in western Oregon and Washington.

Significance. First record as a naturalized plant in Oregon.

POLYGONUM BALDSCHUANICUM Regel (POLYGONACEAE).—Multnomah Co., climbing in trees, cliffs above Oaks Park, bank of Willamette River, SE Portland, 5 Aug 1968, B. G. Brehm s.n. (herbarium of Reed College, 2 sheets).

Previous knowledge. Native to central Asia. *Polygonum baldschuanicum* (syn. *P. aubertii* L. Henry, *Fallopia*) is variously known as lace vine, silver lace vine, Russian-vine and Chinese fleecyvine. It is occasionally planted as an ornamental west of the Cascades in Oregon and Washington, and is a local escape from cultivation in Seattle.

Significance. First collection as a wild plant in Oregon.

—PETER F. ZIKA, Herbarium, Box 355325, University of Washington, Seattle, WA 98195-5325 and EDWARD R. ALVERSON, Herbarium, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331.

PRESIDENT'S REPORT FOR VOLUME 52

Another year has passed in the rich history of the California Botanical Society. Our society was founded by Willis Linn Jepson in 1913 with the first founding meeting at the Oakland Public Museum. Three years later (1916), the first issue of *Madroño* appeared. So, for approximately ninety years, our members have been contributing research and commentary intended to enlighten scientists, academics, managers, and the public as to the wondrous diversity and complexity of the flora and vegetation of our region.

There is, however, another prominent thread in our history, that of conservation (Ewan 1987). It turns out that Jepson became a friend of John Muir and was present at the founding of the Sierra Club in 1892. Jepson apparently recognized that knowledge leads to appreciation, and appreciation to the motivation for conservation. In September, 1913, the International Phytogeographic Excursion (IPE) was held in California and on September 12—five months after the founding of the California Botanical Society—Jepson gave an address at the IPE dinner. His closing words, as related by Ewan (1987), were as follows: “Now there arises a school of botanists, the plant ecologists, who are leading us back to the fields and woods, taking with them the experience of all other schools, and in addition making important use of the observations of the old-time naturalists. California is a glorious field for such work, and we welcome them here to help us appreciate our own flora, and to help Californians to an appreciation of it”.

In 1925, Jepson published his *Manual of the Flowering Plants of California*. At that time, he recorded 3727 native species and 292 species of “alien immigrants” (Jepson 1925). Our most recent flora, *The Jepson Manual* (Hickman 1993) records 5862 species including 1023 “naturalized aliens”, leaving 4,839 native species. So, while the number of recognized native species has grown about 30% since Jepson’s 1925 flora—a number one might expect given some seventy years of continued botanical exploration and systematic investigation—the number of alien species in California grew about 350%! Another way to think about this is that in 1925, non-native species represented about 7% of our wild vascular plants while in 1993, non-native species constituted about 17% of our flora. This increase in numbers of non-native species is really just the tip of the iceberg since a greater concern focuses on a small minority of these species that are highly invasive and capable of wreaking havoc on California’s native plant assemblages (e.g., yellow star thistle, *Centaurea solstitialis*, and Atlantic cord grass, *Spartina alterniflora*).

My digression into our founding heritage and this contrast between today and the past is motivated by a question that all of us perhaps should be asking ourselves. Given this heritage and the spirit of our times, how are we doing? Are we fulfilling our original mission to promote quality botanical research, disseminate this information widely so as to generate appreciation for our flora and vegetation, and are we continuing to build a foundation for the conservation of this biota into the future? I’m happy to say that I think the answer is “yes” and several events that transpired during this past year provide the grist for this viewpoint. It is my pleasure to recount some

of these events and acknowledge several society members who are in part responsible for this favorable situation.

Perhaps the most exciting event that underscores this perspective was the 21st Biennial California Botanical Society Graduate Student Meeting held during a blustery day at the San Francisco State University Romberg Tiburon Bay Conference Center on February 19, 2005. The setting was sublime and there was excellent attendance as 29 graduate student presentations were delivered in two sessions of Systematics, three sessions of Ecology, and one session each of Population Genetics, Paleobotany, and Ethnobotany. There was great representation from most of the major institutions in California and one graduate student traveled from as far away as the University of Washington. Vicente Garcia, the UC Berkeley Graduate Student Representative on the council this year, was a driving force in organizing the event along with a local San Francisco State University Graduate Student Representative, Diana Benner. Debra Hansen, another graduate student from San Francisco State, did a superb job of producing a program introducing the meeting, the schedule, and student presentation abstracts. The presentations were excellent and it was a serious challenge to determine outstanding speakers in all of the subject areas. However, ultimately, the three outstanding speakers were identified: Ms. M.M. Apodaca from California State University Long Beach in Ecology for her talk entitled “Evaluation of two constructed salt marshes in Long Beach, CA through examination of plant percentage cover and plant diversity”; Ms. Abigail Moore of UC Berkeley in Systematics for her presentation entitled “An ETS phylogeny of *Balsamorhiza* and *Wyethia* (Asteraceae)”; and Ms. Katrina Dlugosch from UC Santa Cruz in Population Genetics for her talk entitled “Genetic bottlenecks and rapid evolution in an invasive shrub”. Each of these outstanding speakers was awarded a \$100 prize. The scientific merit of these talks and their relevance to the challenges facing our region bode well for the future of the California Botanical Society.

Later that evening, we held our annual banquet thanks to the organizational effort of Second Vice President Gretchen Lebuhn, a conservation biologist at San Francisco State University. Our host, Dr. Alissa Arp, Director of the Romberg Tiburon Center, was generous in helping to offset our costs for using this fine facility. As always, the opportunity to meet old friends and make new acquaintances flew by far too fast as dinner was served and conversation shifted to individual tables. After making a few introductory comments, I had the pleasure of introducing Dr. Arturo Gomez-Pompa, a long-time Professor of Botany and Plant Sciences at UC Riverside, winner of the prestigious Tyler Prize for Environmental Achievement in 1994, and most recently honored by the UC Regents as a system-wide University Professor. After a long and distinguished career with major contributions to tropical ecology and conservation, Arturo pushed aside retirement to embark upon a new adventure, the founding of an ambitious academic exchange and research program in the biologically rich but economically impoverished state of Vera Cruz in Mexico. He shared his enthusiasm and vision for this new venture, the Centro de Investigaciones Tropicales (Center of Tropical Research, or CITRO),

which is a collaborative effort between UC Riverside and Universidad Veracruzana. Long an advocate for recognizing the importance of indigenous people in the management of tropical forest ecosystems, Arturo described this effort is intended to bring research into practice in solving the real world problems of the people of Vera Cruz while conserving their rich biodiversity. Arturo's passion and dedication were a joy to behold. As hoped, he was a perfect inspirational counter-point to the youthful exuberance demonstrated by the graduate students earlier in the day.

Another great example of our effort to foster dissemination of contemporary botanical research is the series of public lectures put on each year at UC Berkeley following our council meetings. Once again, we have been fortunate to have our First Vice President, Stefania Mambelli of UC Berkeley, organize this series. Last year, the lecture series began with Ray Cranfill of UC Berkeley providing us insights into fern phylogeny, James Wanket of CSU Sacramento then explored the mysteries of Klamath Mountain forest relicts and refugia, Susan Lambrecht of CSU San Jose then presented her excellent work on the costs of reproductive effort in a native blackberry compared to an invasive non-native congener. Jim Shevock of the Californian Cooperative Ecosystems Studies Unit at UC Berkeley raised eyebrows and fascination with the wonders of mosses in a variety of contexts, Scott Stephens provided an insightful description of northwestern Mexican Jeffrey pine forests and its implications for U.S. forest restoration, Elizabeth Wenk of UC Berkeley described the fascinating results of her dissertation research into the physiological distinctions between species distributed on different substrates on a high alpine ridge in the eastern Sierra, and Michelle McMahon of UC Davis examined different floral morphs and their implications in leguminous tribe Amorphaeae. Once again, Vicente García, the Graduate Student Representative, did a wonderful job organizing post-lecture social gatherings in the UC/Jepson Herbarium where a generally excellent turn-out kept the conversation and questions flowing. Thanks again to Stefania and Vicente for their exemplary efforts in the past and the great program underway for 2005–2006. Elizabeth Zacharias, last year's student representative, has also been a great support for the graduate student meeting and the public lecture series. For more information about the exciting new program Stefania has put together, see our web-site (www.calbotsoc.org).

One of the most important accomplishments this past year has been to engineer a smooth transition from John Callaway of the University of San Francisco as *Madroño* editor to John Hunter, affiliated with the UC Davis Herbarium and Center for Plant Diversity. The incredible work of John Callaway to bring a sense of continuity and timeliness to our publication of *Madroño* will long be remembered. However, he also contributed his steady hand to the transition of John Hunter and, as you can see from this issue, John Hunter has already stepped up and is doing an excellent job in keeping *Madroño* on track. The true test of the strength of an organization is the ability to stay fresh and strong in the face of change. We are indeed fortunate to have someone of the caliber of John Hunter step forward to take on this responsibility. I also want to acknowledge that he is not alone. Joining our board of editors this year are Robert E. Preston of Jones & Stokes and Ellen Dean of University of California Davis and EDAW. Jon Keeley continues as an exemplary book editor and Dieter Wilken and Margriet Wetherwax are our noteworthy collection editors. All of these individuals, and the

many individual reviewers and authors, collectively, make *Madroño* an excellent scientific journal.

Another very important contribution to our society is that of Curtis Clark of the Biological Sciences Department at California State Polytechnic University in Pomona and John La Duke at the University of North Dakota. These gentlemen keep our web site maintained.

We also are fortunate to have a vigorous and active council. These are individuals that work behind the scenes to keep the California Botanical Society adaptive and dynamic. They are at the vortex of our efforts to fulfill the mission laid out so long ago by founders such as Willis Linn Jepson. Susan Bainbridge, our corresponding secretary, has simply been invaluable in her depth of knowledge about our operations and creativity in problem solving. Staci Markos, our recording secretary, has been an inspiration with her vision and reliability in keeping communication active and engaged. Roy Buck, our treasurer, has devoted himself to managing our finances in a prudent and responsible way. These three were on the council when I arrived as president. Thank goodness they have been kind enough to stay on and continue to make their wonderful contributions. Bruce Baldwin, our immediate past-president, has also been a mainstay in keeping our organization on track. Two other long time at-large members of the council are Jim Shevock, National Park Service, and Dean Kelch of the U.C. Jepson Herbarium. Both Jim and Dean contribute tremendous experience and depth to our decision making process, as well as taking on several important projects.

Our newest at-large member is Jeffrey Corbin in the Department of Integrative Biology at U.C. Berkeley. Jeff is an active proponent of native grassland restoration. I'm excited to report that yet another example of the society fulfilling its mission is our decision to host a forum at the up-coming international meeting of the Society for Conservation Biology in San Jose from June 24–28, 2006. Our proposed forum will focus on "Ecological Restoration in a changing world: Case studies from California". Our goal is for the presentations at this symposium to be compiled into a special issue of *Madroño*. We are excited at the prospect of this special issue attracting new members and more attention to our society. I further see this as a great way for us to further the conservation mission that is a vital part of our society.

I'm also very pleased to announce that our new Second Vice President, J. Travis Columbus from Rancho Santa Ana Botanic Garden, will be organizing our annual banquet this year in southern California at that venue. The banquet will take place on February 11, 2006, and our very own stalwart, Jon Keeley of the Sequoia and Kings Canyon Field Station with the USGS Western Ecological Research Station in Three Rivers, CA, will be delivering this year's annual banquet address on the topic of "Ecology and Evolution of Fire Prone Ecosystems in California". Jon has an impressive history of publications investigating the influence of fire on the vegetation of California. Given the centrality of this management issue to the southern California community, we are hoping that our southern California colleagues and other interested members of the public will come to hear Jon's entertaining and important scientific observations and perspectives on this critical issue.

Another project we're working on this year is the goal of putting back issues of *Madroño* on-line and, ideally, making recent issues available to our members, possibly through our web site. Bruce Baldwin, Jim Shevock, and

Sue Bainbridge will be working on this important project. Stay tuned!

In summary, I'm not precisely sure what Willis Linn Jepson originally envisioned for the California Botanical Society. My guess is that he didn't foresee the possibilities of the internet, the technological innovations that have broadened the depth and breadth of our research, nor perhaps could he have foreseen the dramatic transformation of our natural environment due to the collective activities of the millions of humans that have settled in our region since his time. Yet, if he were able to adjust to these realities, as we must, my guess is that he would be gratified to see what we have become. In so many ways, we are holding true to the mission—both explicit and implicit—that resulted in our creation. For that, I am thankful. But even today, I'm sure that Jepson would seek to inspire us with his motto: "There is something lost behind the ranges over yonder. Go you there." (Hickman 1993). Indeed, there are still unexplored places. Let us never forget the joy of discovery and the omnipresence of the unknown while we strive to create the foundation of knowledge and

insight that will help our society appreciate and conserve this rich natural legacy that is our ultimate inspiration.

Because of you, the dedicated members of the California Botanical Society, and the efforts of people such as those identified above and many others, our organization continues to flourish. Jepson's dream is still vibrant. Thank you!

MICHAEL VASEY
October, 2005

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EDITOR'S REPORT FOR VOLUME 52

I am pleased to report that during 2005 the number of manuscripts submitted to *Madroño* was comparable to previous years, and that the California Botanical Society has published another volume of *Madroño* reporting research on the flora and vegetation of western North America.

During the first ten months of 2005, 28 manuscripts were submitted. Of these manuscripts, two were rejected, seven had major revisions requested, eleven were accepted with minor revisions, and eight manuscripts are still being reviewed. Of those accepted with minor revisions, seven were published in this volume. The interval from submission to publication has been approximately nine months long. During 2005, eight book reviews and 18 noteworthy collections (revising the geographic range of 66 species) also were submitted, and 24 of these have already been published.

During this past year, I have been repeatedly struck by how *Madroño* both supports and is a product of the botanical community of western North America. Volume 52 reported the research of 84 different authors. These au-

thors were aided by numerous reviewers, an editorial board, Jon Keeley (Book Review Editor), Dieter Wilken (Noteworthy Collections Editor), Margariet Wetherwax (Noteworthy Collections Editor), Steve Timbrook (Compiler for Annual Index), Annielaurie Seifert and her colleagues at Allen Press, the Executive Council of the California Botanical Society (who, in addition to their regular support of this journal's production and distribution, are working to make *Madroño* available on-line and to produce a special conservation issue), and John Callaway, who produced 52(1) and helped throughout the year. All of these individuals deserve to be recognized and thanked for their contributions to *Madroño*. I also want to thank everyone not only for their contributions to Volume 52, but for being so patient and gracious during this past year as I grew into the role of editor. Thanks.

I look forward to helping the botanical community of western North America produce *Madroño* in the coming year.

JOHN C. HUNTER

REVIEWERS OF MADROÑO MANUSCRIPTS 2005

Jeremy Ahouse
Joe Antos
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DEDICATION



HAROLD HEADY

In 1951 Harold Heady left a tenured position at Texas A&M to join the faculty in University of California Berkeley's School of Forestry as an Assistant Professor in Range Management. The more than thirty years of productive research and teaching that followed showed the wisdom of that potentially risky move.

At Berkeley Harold joined two other former students (Harold Biswell and Arnold Schultz) of the eminent prairie ecologist John Weaver. Because Weaver was Frederick Clements' most influential student, academic dogma suggests that Berkeley would become a satellite of neo-Clementian thought. It didn't work out that way, in part because of the Mediterranean environment and in part because of the unique group of ecologists who were working in the Bay Area in the 1950s.

Harold was born on a ranch in the Snake River Plains of Idaho and attended the University of Idaho, where he was later honored as outstanding alumnus and by establishment of the Harold F. Heady Chair in Range Management. He then moved east to earn an M.S. from the New York State College of Forestry; his thesis was a comprehensive local flora. During World War II, except for a very brief stint in the Navy, he taught range management at Montana State University. While holding faulty positions at MSU and later at Texas A&M he simultaneously earned a Ph.D. at the University of Nebraska and helped found the Society for Range Management (SRM), serving as its first Secretary-Treasurer. He was later president of the SRM and has received all of its major awards.

When Harold arrived at Berkeley in 1951 to fill the

position created by recently retired Arthur Sampson, the University had just purchased the Hopland Field Station and was expanding range management on the Davis campus. This led to many productive research collaborations and years of joint teaching on both the Berkeley and Davis campuses. Along with Station superintendent Al Murphy, Harold immediately set to work on a comprehensive floristic inventory at Hopland. This work included many permanent photo stations and establishment of two protected areas. Their thorough floristic inventory has recently served as the basis for an analysis of floristic change and effects of land use. The joint teaching programs in range management at Berkeley and Davis developed separately after the mid-1970s and have produced many influential graduates, including several deans and department chairs.

Harold's research focused on the ecology and management of the California grassland. He was appointed at Berkeley to mainly bring a highly quantitative approach to the program, but as is too rare today, he was a broadly trained botanist. Several of his research papers are landmarks of organized critical thinking and one of the tasks of current range scientists, often to our dismay, is to remind students to "... read what Heady wrote about this in ...". Examples are his work with the height/weight relationships of grasses, still relevant to current problems with grazing utilization standards; specialized grazing systems; vegetation sampling methods; inter and intra annual variation in species composition; selective grazing; and livestock/wildlife interactions. Two projects illustrate Harold's approach to research. He followed the effects of a

woodland type conversion at Hopland for 19 years. The analysis involved a complex experimental design that could not have been completed without the invention of modern computer-based methods during the course of the study. Most of us involved with the study believe that Harold knew all along that this would happen. A second study established a series of plots over a 300-mile transect to examine the effects of natural mulch on productivity and composition of grassland. Data from this robust study are still being analyzed today and formed the basis for what is now the most important technique for monitoring livestock grazing intensity on annual rangelands.

It is noteworthy that Harold quickly saw that the California grassland didn't fit the standard Clementian models for succession and range condition evaluation. His research into the effects of mulch on production and composition, the relationships between grassland species composition and annual weather, and the small-scale patterns of annual plant interactions over short time scales were all used to adapt the general predictive models to the realities of Californian environment. This approach placed good predictive science into the context of a continuing need for practical management. Possibly the most important example of the fit between Harold and the grassland

is that its annual cycle freed up the fall for hunting and fishing.

For much of his career Harold was a major player in international resource management. He loves foreign travel, usually to remote locations, and spent sabbaticals (with Guggenheim and Fulbright support) in Kenya, Saudi Arabia, and Australia. While in Kenya he turned an enforced stay in the hospital and local travel restriction into his landmark monograph *Range Management in East Africa*. His textbook *Rangeland Management* has been widely used and available as a recent third edition. His other synthetic works include several book chapters on the California grassland and two analyses of the Vale range improvement project in eastern Oregon. After his retirement from UC in 1983 he continued to travel extensively, collaborate on research, write books and articles, and of course still spends every fall hunting.

JAMES W. BARTOLOME
University of California, Berkeley
Department of Environmental Science,
Policy and Management
Berkeley, CA 94720-3114
jwbart@nature.berkeley.edu

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